VEGETATION CLASSIFICATION AND SURVEY

International Association for Vegetation Science (IAVS)

Vegetation Classification and Survey 6: 221–246
doi: 10.3897/VCS.149158

RESEARCH PAPER

CLASSIFICATION OF EUROPEAN FORESTS

Epiphytic lichen communities in old-growth beech forests of western Ukraine

Oleksandr Y. Khodosovtsev[1,2], Jan Vondrák[3,4], Anna A. Kuzemko[5]

1 *Botany Department, Kherson State University, Kherson, Ivano-Frankivsk, Ukraine*
2 *Department of Phycology, Lichenology and Bryology, M.G. Kholodny Institute of Botany, NAS of Ukraine, Kyiv, Ukraine*
3 *Herbarium, Institute of Botany of the Czech Academy of Sciences, Průhonice, Czech Republic*
4 *Faculty of Science, University of South Bohemia, České Budějovice, Czech Republic*
5 *Department of Geobotany and Ecology, M.G. Kholodny Institute of Botany, NAS of Ukraine, Kyiv, Ukraine*

Corresponding author: Oleksandr Y. Khodosovtsev (khodosovtsev@gmail.com)

Academic editor: Wolfgang Willner ♦ **Linguistic editor:** Hallie Seiler
Received 9 February 2025 ♦ **Accepted** 3 October 2025 ♦ **Published** 25 November 2025

Abstract

Aims: To revise the syntaxonomy of epiphytic lichen communities on *Fagus sylvatica* from old-growth beech forests in the Carpathians and adjacent uplands, in particular (1) to identify the main syntaxonomic units and reveal their ecological, structural, and compositional peculiarities; (2) to assign the associations to higher-rank syntaxa; (3) to define the position of the resulting syntaxonomic units in the system of syntaxa of lichen communities of Europe; and (4) to evaluate the potential use of epiphytic lichen communities on beech trees as indicators of the ecological integrity of forest habitats. **Study area:** Ukrainian Carpathians, Roztochchia, Podillia, and Khotyn uplands. **Methods:** 230 relevés of lichen communities from western Ukraine and data from literary sources (reference data) were classified using the modified TWINSPAN algorithm implemented in JUICE software in two steps, identifying units of higher and then lower rank consecutively. **Results:** The first step of the analysis resulted in seven clusters which were mainly interpreted as classes or orders. The second step of the analysis resulted in 20 units of association or unranked community level. 12 of these were recorded in the study area and included 267 lichen species. **Conclusions:** Epiphytic lichen communities on *Fagus sylvatica* in the old-growth beech forests of Western Ukraine are divided into five classes: *Agonimietea repletae* (a new class encompassing lichen communities occurring on exposed roots and the bases of old tree trunks with smooth bark), *Arthonio radiatae-Lecidelletea elaeochromae*, *Hypogymnietea physodis*, *Neckeretea complanatae* and *Physcietea*, and 12 assocations or unranked communities. The order *Agonimietalia repletae*, the alliances *Biatorion radicicolae* and *Dictyocatenulation albae*, and five associations are newly described here. The provisional alliance *Biatorion vernalis* is proposed for epiphytic lichens on mosses.

Taxonomic reference: Nimis et al. (2018).

Abbreviations: EUNIS = European Nature Information System; EVC = EuroVegChecklist; ICPN = International Code of Phytosociological Nomenclature; UNESCO = United Nations Educational, Scientific and Cultural Organization; OD = Original diagnosis.

Keywords

Agonimietea repletae, *Biatorion radicicolae*, *Biatorion vernalis*, biodiversity, *Dictyocatenulation albae*, *Fagus*, *Graphidion scriptae*, hotspot, indicator, *Parmelion physodis*, *Xanthorion parietinae*, syntaxonomy

PENSOFT

Copyright *Oleksandr Y. Khodosovtsev et al.* This is an open access article distributed under the terms of the Creative Commons Attribution License (CC-BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

Introduction

Ukraine is one of the few countries in Europe with large areas of primeval beech forests. Ancient Carpathian beech forests were included in the UNESCO World Heritage List due to their enormous importance and uniqueness (e.g. Commarmot et al. 2013). The Ukrainian Carpathians have significant lichen diversity. Some areas are a key for diversity of forest lichens in Europe. The biodiversity survey revealed 387 corticolous and lignicolous lichens and allied fungi in five one-hectare plots within the Uholka massif of the old-growth beech forest in the Carpathian Biosphere Reserve, with a maximum of 228 species per hectare (Vondrák et al. 2018; Malíček et al. 2018), a record for epiphytic lichen diversity within Central Europe. Moreover, Carpathian old-growth beech forests host many lichens that are indicators for the ecological integrity of forest habitats (Kondratyuk et al. 1997; Kondratyuk and Coppins 1999; Dymytrova et al. 2013). The most famous of these are *Lobaria pulmonaria*, *Leptogium saturninum*, *Parmeliella triptophylla*, and *Sticta fuliginosa*. According to preliminary estimates, 331 species of lichens are associated with the bark of *Fagus sylvatica* in Ukraine (Hurtado et al. 2023).

Nevertheless, the available information about epiphytic lichen communities in old-growth beech forests is extremely limited. The study of epiphytic lichen communities in European beech forests was initiated almost simultaneously with the establishment of the phytosociological methodology. Nearly a century ago, Hilitzer (1925) described the first associations of epiphytic lichens from forest habitats in the Czech Republic. He identified some of them on the bark of *Fagus sylvatica* in beech forests. The species composition of the communities described by Hilitzer exhibited significant similarity, which later prompted Barkman (1958) to revise the scope of these associations and synonymize them. Subsequently, they were assigned to the alliance *Graphidion scriptae* (Ochsner 1928; Barkman 1958; Klement 1955; Drehwald 1993; Mucina et al. 2016). It should be noted that communities typically associated with conifers (e.g. *Abies*, *Picea*) were also partially found in mixed beech-fir forests (Hilitzer 1925). These acidophilous communities were grouped under the alliance *Parmelion physodis* (von Krusenstjerna 1945; Mucina et al. 2016). Hilitzer (1925) was a pioneer in studying communities with *Lobaria pulmonaria*. Later, these associations were included in the alliance *Lobarion pulmonariae* (Ochsner 1928) based on a survey of epiphytic lichen communities in Switzerland. A thorough analysis of the syntaxa described by Hilitzer is provided in the seminal work of Barkman (1958), who made the lectotypification and synonymization of Hilitzer's associations.

Thereafter, the geographic scope of epiphytic lichen associations related to European beech forests was expanded by Klement (1955). Unfortunately, his work includes only synoptic tables which are difficult to integrate into modern phytosociological analyses. A relatively comprehensive analysis of "northern" epiphytic communities in Scandinavian countries is presented in Almborn (1948). Only some of Almborn's associations have been accepted, and their nomenclature has been aligned with the rules of the ICPN (Theurillat et al. 2021). Several new epiphytic lichen communities on beech were published in Barkman (1958). The distribution of several lichen associations related to beech forests or the bark of beech is also documented in well-known syntaxonomic syntheses of lichen vegetation for Germany (Wirth 1980, 1995; Drehwald 1993), Hungary (Gallé 1976), and the United Kingdom (James et al. 1977).

In general, lichen communities on beech trees in European forests have been assigned to only two classes: *Arthonio radiatae-Lecidelletea elaeochromae* on the neutral, smooth bark of deciduous trees, and *Hypogymnietea physodis* on the acidic bark of deciduous and coniferous trees. Moss-lichen communities in the humid forests of Europe of the *Lobarion pulmonariae* alliance were considered part of the *Neckeretea complanatae* class.

The high diversity of epiphytic lichens in the unique primary ecosystems of Ukrainian Carpathian beech forests and adjacent areas should also result in a high level of syntaxonomic diversity. However, according to the literature (Klement 1955), only one association, *Pyrenuletum nitidae*, has been reported from the beech forests of Ukraine. Our study aims to fill this gap. Moreover, it reflects a renewed focus on lichen communities in Central European beech forests after being initiated 100 years ago by Alfred Hilitzer. This study aimed to revise the syntaxonomy of epiphytic lichen communities on *Fagus sylvatica* from old-growth beech forests in the Carpathians and adjacent uplands, in particular (1) to identify the main syntaxonomic units and reveal their ecological, structural, and compositional peculiarities; (2) to assign the associations to higher-rank syntaxa; (3) to define the position of the resulting syntaxonomic units in the system of syntaxa of lichen communities of Europe; and (4) to evaluate the potential use epiphytic lichen communities on beech trees as indicators of the ecological integrity of forest habitats.

Study area

The old-growth beech forests of the Ukrainian Carpathians are located within the core and buffer zones of the UNESCO World Heritage Site "Primeval Beech Forests of the Carpathians" (https://whc.unesco.org/en/list/1133/documents/). Our study focuses specifically on several large forest stands: Gorgany, Shyrokyi Luh, Irshavka, Velykyi Dil, and Synevyr within the Carpathians, as well as the Roztochchia, Podillia, and Khotyn uplands (Figure 1). These forests are classified as primeval or quasi-primeval by Stoyko (2002) and Commarmot et al. (2013). Some data were also collected from old-growth beech forests at the timberline adjacent to the Carpathian grasslands (*polonynas*) Borzhava, Bozna, Kuk, and Krasna. Additionally, we studied three natural old-growth beech forest sites located outside the Carpathians, in the Roztochchia

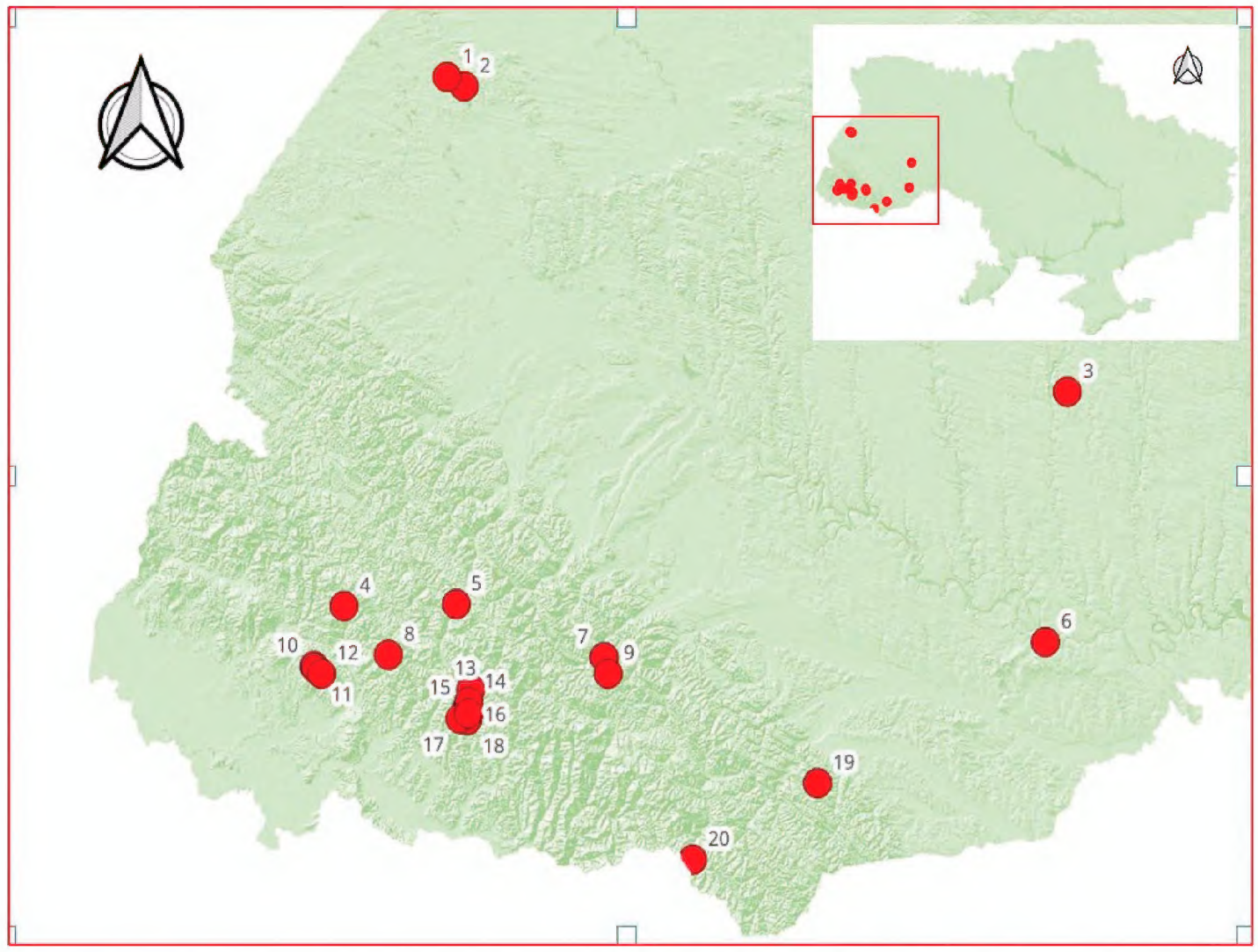

Figure 1. The stands of old-growth beech forest investigated in this study: 1–2 – Roztochchia (Yavorivskyi National Nature Park), 3 – Podilia Upland (Satanivska Dacha, Podilski Tovtry National Nature Park), 4 – polonyna Borjava, 5 – Synevir National Nature Park, 6 – Khotyn upland, 8 – polonyna Kuk (Zacharovanyi Kray National Nature Park), 7, 9 – Gorgany National Nature Park, 10–12 – Zacharovanyi Kray National Nature Park, 13 – polonyna Krasna (Synevir National Nature Park), 14–18 – Shyrokyi Luh (Carpatian Biosphere Reserve), 19 – Mt Bozna (Vyzhnytskyi National Nature Park), 20 – beech reserve near village Burkut.

(Yavorivskyi National Nature Park), Podillia (Satanivska Dacha), and Khotyn uplands. According to the EUNIS habitat classification (Chytrý et al. 2020), the studied old-growth beech forests belong to three habitat types: *Fagus* forests on non-acid soils (T17), *Fagus* forests on acid soils (T18), and temperate mountain forests of *Abies* (T32).

Methods

Epiphyte concept

Abstract units of epiphyte communities, representing particular habitats delimited at fine spatial scales and supporting bryophyte, lichen, or other "cryptogamic" communities, are considered as syntaxa in the current edition of the ICPN (Theurillat et al. 2021). We recognized lichen communities as an independent part of the vegetation continuum (Khodosovtsev et al. 2023). Under the term "epiphytic lichens," we included all lichen communities occurring on the integumentary tissues of plants (epidermis, periderm, or rhytidome) and dead wood (xylem), particularly on the bark and roots of trees, in cracks in the bark, on living leaves of conifers (epiphyllous), and on bryophytes. This study focuses on the lichen communities on beech. Corticolous bryophyte-lichen or lichen-bryophyte communities, as well as lichen communities on conifers, were not the focus of this research.

Field data and sampling

Field research was conducted between 2019 and 2024 in the Ukrainian Carpathians and allied adjacent uplands within the Chernivtsi, Ivano-Frankivsk, Khmelnytsky, Lviv and Zakarpattia oblasts, focusing on natural old-growth beech forests.

Ecologically uniform areas were selected for the phytosociological surveys. Under optimal conditions, each beech included several relevés (ranging from one to four per tree): (1) at the base of the tree or on exposed living root systems; (2) on mosses at the base or trunk; (3) on the smooth bark of the tree (on different sides of the trunk if visually distinct communities were observed); and (4) on tree branches (very rarely, relevés were also taken from bark and branches of living fallen trees). Typically, relevés sizes on the trunk ranged from 0.3 m^2 (0.2 m × 1.5 m along the trunk) for young and medium-age trees to 0.75 m^2 (0.5 m × 1.5 m along the trunk) for old trees. However, in some cases, the relevé sizes were different, for example, in the case of smaller patches of lichen communities on bark surrounded by mosses. The plots on root systems were much smaller, typically 0.02 m^2 (0.1 m × 0.2 m along a root). Similar plot sizes were used for communities on bryophytes, as well as for branches and very young trees, where the plot size was 0.02 m^2 (0.05 m × 0.4 m along a branch). For each location, we recorded the following parameters: geographic coordinates, altitude, aspect, total

lichen cover (%), and the individual cover of each identified lichen species (%). Typically, we selected relevés that contained only lichens directly on bark excluding communities with vascular plants and bryophytes, with the exception of epiphytic lichen communities on mosses and liverworts over the bark. Bark-dwelling non-lichenized fungi, free-living microalgae, cyanobacteria, non-lichenized fungi, and lichenicolous fungi were not included in the species list of relevés, nor were species of bryophytes which were a substrate for hyperepiphytic lichen communities.

The total number of relevés used for the analysis was 293, with 230 of them from western Ukraine. The rest were digitized from literary (reference) sources. These comprised:

1) Lectotype and four additional relevés from the original diagnosis (OD) dataset of the association *Nephrometum belli* (Hilitzer 1925) Barkman 1958 (= populations des Stictates Hilitzer 1925) (Hilitzer 1925; Barkman 1958). This association is a lectotype of the alliance *Lobarion pulmonariae* (Ochsner 1928; Barkman 1958). This alliance is the lectotype of the order *Antitrichietalia curtipendulae* (class *Neckeretea complanatae*) (Mucina et al. 2016).
2) Lectotype of the association *Physcietum adscendentis* Frey et Ochsner 1926 (Ochsner 1928; Barkman 1958). This association is a lectotype of the alliance *Xanthorion parietinae* Ochsner 1928. This alliance is the type for the order *Physcietalia* and it, in turn is type for the class *Physcietea* Tomaselli et DeMicheli 1952 (Mucina et al. 2016).
3) Lectotype and two additional relevés from the OD dataset of the association *Lecanoretum carpinea montanum* Barkman 1958 (Barkman 1958). It is a lectotype for the alliance *Lecanorion carpineae* Ochsner 1928 corr. Barkman 1958.
4) Lectotype and three additional relevés from the OD dataset of the association *Pseudevernio furfuraceae-Hypotrachynetum afrorevolutae* (Almborn 1948) Delzenne and Gehu 1978 (= *Parmelietum revolutae* (Almborn 1948) Barkman 1958, *Parmelia revoluta* – communities Almborn 1948) (Almborn 1948; Delzenne and Gehu 1978; van Haluwyn 2010). It is the lectotype of the *Parmelion perlatae* (Barkman 1958) James et al. 1977 (= *Parmelion caperatae* Barkman 1958) (Mucina et al. 2016).
5) Lectotype of the association *Parmelietum furfuraceae* Hilitzer 1925 (Hilitzer 1925; Barkman 1958). It is the lectotype of the alliance *Parmelion furfuraceae* Barkman 1958 (Barkman 1958). This alliance is the type for the order *Parmelietalia physoso-tubulosae* Barkman 1958, current name *Alectorietalia* Dahl et Hadač in Klika et Hadač 1944. This order is the type for the class *Alectorietea* Hadač 1962, current name *Hypogymnietea physodis* Follmann 1974 (Mucina et al. 2016).
6) Lectotype and one additional relevé from the OD dataset of the association *Parmelietum physodo-sulcatae* von Krusenstjerna 1945 (von Krusenstjerna 1945; Mucina et al. 2016). It is the lectotype of the alliance *Parmelion physodis* von Krusenstjerna 1945 (Mucina et al. 2016).
7) Lectotype and 19 additional relevés from the OD dataset of the association *Pyrenuletum nitidae* Hilitzer 1925 (Hilitzer 1925; Barkman 1958). It is the lectotype for the alliance *Graphidion scriptae* Ochsner ex Felföldy 1941. The last alliance is the type for the order *Arthonietalia radiatae* Barkman 1958, current name *Graphidetalia scriptae* Hadač in Klika et Hadač 1944. The last order is the type for the class *Arthonio radiatae-Lecidelletea elaeochromae* Drehwald 1993 (Mucina et al. 2016).
8) Holotype and two additional relevés from the OD dataset of the association *Hypocenomycetum stoechadianae* Abbassi Maaf et Roux 1978 (Abbassi Maaf et Roux 1987). It is the lectotype for the alliance *Agonimion* octosporae Bricaud et Roux in Bültmann et al. 2015. This alliance is the type for the order *Bacidinetalia phacodis* Bricaud et Roux in Bültmann et al. 2015 (Bültmann et al. 2015).
9) Holotype and four additional relevés from the OD dataset of the association *Anaptychio ciliaris-Lobarietum pulmonariae* Zhuravleva et al. 2004 (Zhuravleva et al. 2004).
10) Holotype of the association *Parmelietum trichoteroscorteae* Barkman 1958 (Barkman 1958).
11) Lectotype and three additional relevés from the OD dataset of the association *Pertusarietum amarae* Hilitzer 1925 (Hilitzer 1925; Barkman 1958).
12) Holotype and four additional relevés from the OD dataset of the association *Porinetum carpineae* Barkman 1958 (Barkman 1958).
13) Lectotype and one additional relevé from the OD dataset of the association *Thelotremetum lepadinii* Hilitzer 1925 (Hilitzer 1925, Barkman 1958).
14) Holotype and two additional relevés from the OD dataset of the association *Opegraphetum diaphorae* Barkman 1958 (Barkman 1958).

Identification of lichens

We collected samples of lichens that cannot be identified in the field. These lichens were identified using microscopy techniques according to standard procedure (Smith et al. 2009; Nimis 2025). Species nomenclature follows the lichen checklist for the Alps (Nimis et al. 2018). For species not included in Nimis et al. (2018), which are usually a small fraction of recently described species, we use their original names.

Data analyses

Relevés were stored in the TURBOVEG software (Hennekens and Schaminée 2001). We used the modified TWINSPAN algorithm (Roleček et al. 2009) for data

clustering in the JUICE software (Tichý 2002), with pseudospecies cut levels set at 0–5–25 and the average Sørensen index as the dissimilarity measure. The resulting units were evaluated for quality using the Sharpness index (Chytrý and Tichý 2003) and average Whittaker beta diversity (Kuzemko 2016). A two-step analysis was performed. In the first step, we analysed the whole dataset and identified the main clusters to understand the differentiation at the level of highest syntaxa (classes and orders). In the second step, we performed clustering separately within each major unit defined during the first step, thus obtaining lower-ranked units (associations and unranked communities). Species were considered diagnostic if they had a *phi* coefficient greater than or equal to 0.25 and highly diagnostic if the *phi* coefficient was greater than or equal to 0.50 (Chytrý et al. 2002). Species with a percentage frequency above 40% were classified as constant, while dominant species were defined as those with a cover exceeding 25%. Character species were selected mainly for alliances, while diagnostic species were identified for associations within a specific class (species with $phi \geq 0.25$). The diagnostic species of classes follow FloraVeg.EU (https://floraveg.eu/vegetation/).

Ordination analysis was performed using R version 4.5.1 (R Core Team 2025). We analysed lichen species composition using nonmetric multidimensional scaling (NMDS) by applying the '*metaMDS*' function from the '*vegan*' package (Oksanen et al. 2018) to the occurrence matrices of species for each plot with species-specific cover.

Characteristics of vegetation units

The description of each resulting vegetation unit includes the following components (Khodosovtsev et al. 2022): synecology, diagnostic species, dominant species, constant species, symphysiognomy, and synfloristics. Ecological features of the substrate and microclimate of the communities, considered important by Klement (1955) and Wirth (1972, 1995), were also incorporated. The main ecological characteristics of the communities follow the framework proposed by Khodosovtsev et al. (2022). However, for humidity, based on substrate moisture, we introduced the category "substrate hygrophilous" to describe epiphytic communities on bryophytes. The following categories were used to classify clusters: (1) species-poor (total species list of a cluster includes 2 to 30 species); (2) of medium species-richness (31–60 species); (3) species-rich (61–90 species); and (4) hotspot (> 90 species). Additionally, information on rare lichen species were included.

Syntaxonomy

New lichen syntaxa were described in accordance with the requirements and recommendations of the ICPN (Theurillat et al. 2021). The syntaxonomy of alliances, orders, and classes follows the framework provided by Mucina et al. (2016). Holotypes for the new associations were selected based on the criteria outlined in Khodosovtsev et al. (2022). The original names of associations used in the text primarily follow the nomenclatural principles established by Barkman (1958). The lichen communites on bryophytes may rather be considerd synusiae, which are not currently treated in the ICPN.

Results

The results are arranged in two blocks according to the two-step analysis. In the first, all relevés were analysed together and divided into seven clusters at the high syntaxa level. In the second, the clusters were analysed separately and divided into sub-clusters at the lower level.

First step of analysis

The dataset was divided into seven large clusters (Figure 2) corresponding to units of high syntaxonomical level. The analysis divided the data into two groups A–C and D–G. The first group mainly includes relevés on the root system of trees, and the second group includes relevés on the trunk and branches. Clusters A and B include communities of exposed or shaded roots and trunk bases. These clusters do not include any data from the literature. Clusters C and D comprised lichen communities on bryophytes, which in turn grow on tree bark. Cluster D corresponds to the alliance *Lobarion pulmonariae* (lichen-bryophyte class *Neckeretea complanatae*). Cluster C does not include any reference data. Clusters E–G mainly include communities on the bark of the trunk and branches, with each cluster representing a class of lichen communities. Cluster E includes the type relevés of *Anaptychio ciliaris-Lobarietum pulmonariae*, *Lecanoretum carpinea montanum*, *Physcietum adscendentis*, and *Parmelietum trichotero-scorteae*. We interpreted this cluster as belonging to the class *Physcietea* (Mucina et al. 2016). The associations *Parmelietum furfuraceae*, *Pseudoevernio furfuracea-Hypotrachynetum afrorevolutae*, and *Parmelietum physodo-sulcatae* fall into the cluster F. This cluster is assigned to the class *Hypogymnietea physodis* (Mucina et al. 2016). The cluster G includes the nomenclatural types of the associations *Hypocenomycetum stoechadianae*, *Opegraphetum diaphorae*, *Pertusarietum amarae*, *Porinetum carpineae*, *Pyrenuletum nitidae*, and *Thelotremetum lepadinii*. This cluster belongs to the class *Arthonio radiatae-Lecidelletea elaeochromae* (Mucina et al. 2016). The resulting units had different levels of internal heterogeneity, which did not allow us to obtain final units of a lower level during the first stage of analysis. Clusters, A, C and D were homogenous, while clusters B and E–G were heterogenous and divided in the second step of the analyses.

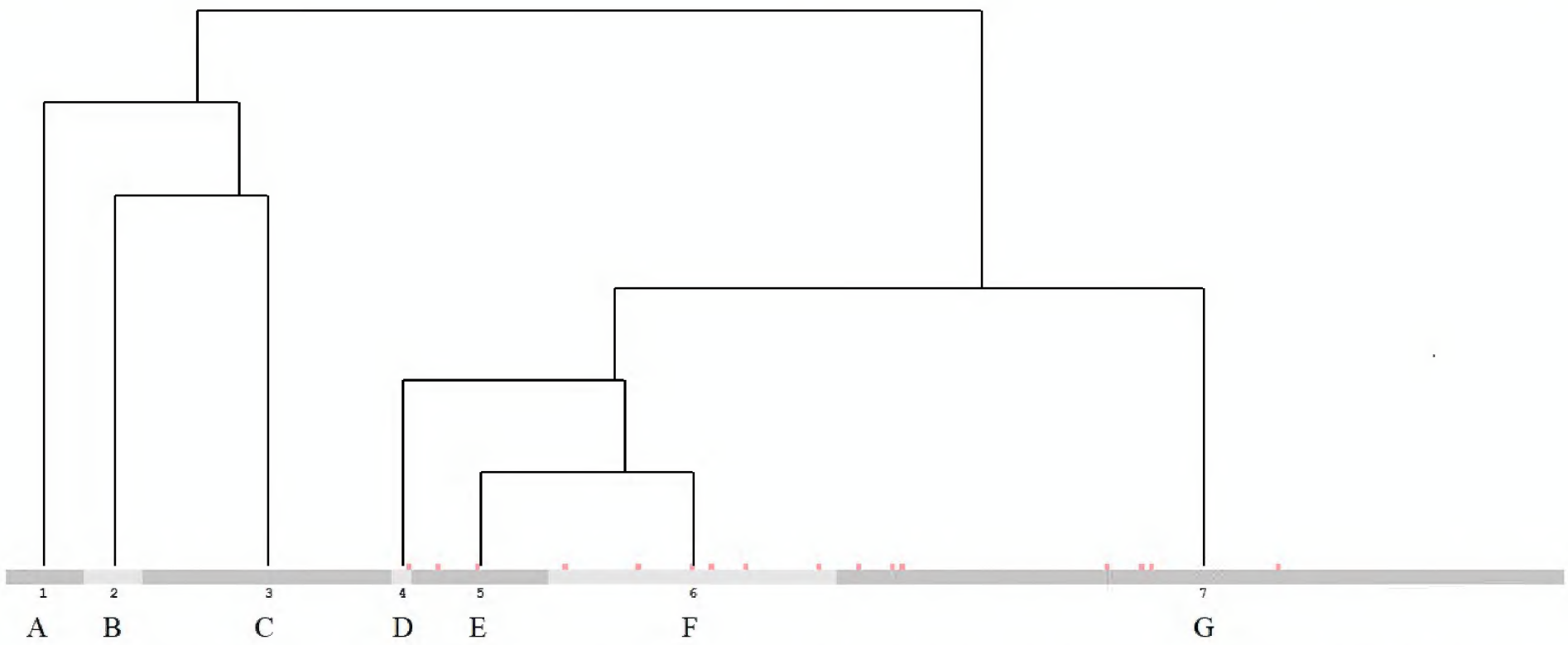

Figure 2. Dendrogram of the first step cluster analysis. Red dots represent nomenclatural types from the reference data.

Second step of analysis

Twenty clusters that mainly represent associations were obtained after the final clustering (Table 1, Supplementary material 5). Of these, 11 units included our original data only, 1 cluster included both our data and data from the OD dataset, and 8 clusters included only reference data.

Table 1. Synoptic table of lichen communities on *Fagus sylvatica* in the old-growth beech forests of western Ukraine and reference European communities. The numbers indicate the percentage frequency, and the shading indicates fidelity (dark gray shading shows values of the phi coefficient ≥ 0.5, light gray ≥ 0.25). * species reported only in reference data.

Cluster number (total 20)	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**
Code of cluster	**A**	**B1**	**B2**	**C**	**D**	**E1**	**E2**	**E3**	**E4**	**E5**	**F1**	**F2**	**F3**	**F4**	**F5**	**G1**	**G2**	**G3**	**G4**	**G5**
Number of relevés (total 293)	**16**	**12**	**12**	**31**	**4**	**5**	**3**	**2**	**6**	**17**	**7**	**2**	**8**	**22**	**15**	**3**	**51**	**27**	**9**	**45**
Biatora chrysantha	81	.	25	29	.	.	.	.	.	.	.	.	.	14	13	.	2	.	.	2
Biatora radicicola	75	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Porpidia macrocarpa	31	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Caloplaca sorocarpa	31	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Lepraria jackii	31	.	.	.	.	.	.	.	.	.	.	.	.	9	.	.	.	.	11	4
Catinaria atropurpurea	25	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2
Gyalideopsis helvetica	25	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Dictyocatenulata alba	.	83	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	11	.
Arthonia helvola	.	50	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	11	4
Arthonia spadicea	.	33	.	3	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	2
Bacidia subincompta	13	.	58	10	.	.	.	.	.	.	.	.	.	5	7	.	2	.	.	2
Coenogonium pineti	.	25	58	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	7
Porina leptalea	.	.	42	.	.	.	.	.	.	.	.	.	.	.	.	.	4	.	.	16
Gyalecta herculina	6	.	25	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Biatora vernalis	.	8	8	52	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	7
Strigula stigmatella	.	17	.	39	.	.	.	.	.	.	.	.	.	.	.	.	12	.	.	2
Peltigera praetextata	.	.	.	19	100	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
**Sticta fuliginosa*	.	.	.	.	75	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
**Sticta sylvatica*	.	.	.	.	75	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cetrelia cetrarioides	.	.	.	3	50	.	.	.	.	.	.	.	25	5	7	.	.	.	.	.
Cetrelia olivetorum	.	.	.	.	25	.	.	.	.	.	.	.	.	.	13	.	.	.	.	.
Heterodermia speciosa	.	.	.	.	25	.	.	.	.	.	.	.	.	.	7	.	.	.	.	.
**Nephroma resupinatum*	.	.	.	.	25	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
**Nephroma bellum*	.	.	.	.	25	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Anaptychia ciliaris	.	.	.	.	.	100	.	50	33	.	14	.	.	5	20	.	.	.	.	.
Physconia detersa	.	.	.	.	.	80	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Melanelixia subargentifera	.	.	.	.	.	80	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Physconia perisidiosa	.	.	.	.	.	80	.	.	33	.	.	.	.	.	27	.	.	.	.	.

Cluster number (total 20)	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Code of cluster	**A**	**B1**	**B2**	**C**	**D**	**E1**	**E2**	**E3**	**E4**	**E5**	**F1**	**F2**	**F3**	**F4**	**F5**	**G1**	**G2**	**G3**	**G4**	**G5**
Number of relevés (total 293)	**16**	**12**	**12**	**31**	**4**	**5**	**3**	**2**	**6**	**17**	**7**	**2**	**8**	**22**	**15**	**3**	**51**	**27**	**9**	**45**
**Rostania occultata*	.	.	.	.	.	60	.	.	.	.	.	.	.	.	.	.	.	.	.	.
**Parainoa subconcolor*	.	.	.	.	.	40	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Physcia aipolia	.	.	.	.	.	40	.	50	.	12	.	.	.	.	.	.	.	.	.	.
Caloplaca cerina	.	.	.	.	.	.	100	.	33	.	.	.	.	.	.	.	.	.	.	.
Arthonia radiata	.	.	.	.	.	.	100	.	17	18	.	.	.	14	.	.	27	.	.	4
Lecanora carpinea	.	.	.	.	.	.	100	.	33	29	.	.	.	9	20	.	2	.	22	.
**Rinodina polyspora*	.	.	.	.	.	.	33	.	.	.	.	.	.	.	.	.	.	.	.	.
Leptogium saturninum	.	.	.	3	.	20	.	50	.	.	.	.	.	.	.	.	.	.	.	.
Xanthomendoza fulva	.	.	.	.	.	.	.	50	17	.	.	.	.	.	7	.	.	.	.	.
Collema nigrescens	.	.	.	.	.	.	.	50	.	.	.	.	.	.	13	.	.	.	.	.
Flavoparmelia caperata	.	.	.	.	.	.	.	50	.	6	.	.	.	.	.	.	.	.	.	.
**Ramalina fastigiata*	.	.	.	.	.	.	.	50	.	.	14	.	.	9	7	.	.	.	.	.
**Parmotrema perlatum*	.	.	.	.	.	.	.	50	.	.	.	.	.	.	.	.	.	.	.	.
**Hypotrachyna revoluta*	.	.	.	.	.	.	.	50	.	.	.	.	.	.	.	.	.	.	.	.
Punctelia subrudecta	.	.	.	.	.	.	.	50	.	12	.	.	.	.	.	.	.	.	.	.
Lepra albescens	.	.	.	.	.	.	.	50	17	.	14	.	.	5	7	33	.	.	.	.
Physcia tenella	.	.	.	.	.	.	.	.	67	12	.	.	.	5	.	.	.	.	11	.
Rinodina griseosoralifera	.	.	.	.	.	.	.	.	50	.	.	.	.	9	.	.	.	.	.	.
Caloplaca turkuensis	.	.	.	.	.	.	.	.	50	.	.	.	.	.	7	.	.	.	.	.
Pertusaria albescens	.	.	.	.	.	.	.	.	33	.	.	.	.	.	.	.	.	.	.	.
Lecanora saligna	6	.	.	.	.	.	.	.	33	.	.	.	.	.	.	.	.	.	.	.
Gyalecta fagicola	.	.	.	.	.	.	.	.	33	.	.	.	.	.	13	.	.	.	.	.
Scoliciosporum chlorococcum	.	.	.	.	.	.	.	.	33	12	.	.	.	9	.	.	4	.	.	.
Xanthoria parietina	.	.	.	.	.	.	.	50	33	41	.	.	.	.	7	.	.	.	.	.
Scoliciosporum sarothamni	.	.	.	.	.	.	.	.	.	35	.	.	.	14	.	.	4	.	.	.
Candelaria concolor	.	.	.	.	.	.	.	50	.	35	.	.	.	.	.	.	2	.	.	.
Physcia stellaris	.	.	.	.	.	.	.	.	.	29	.	.	.	5	.	.	.	.	.	.
Evernia prunastri	.	.	.	.	.	.	.	50	17	.	100	50	25	.	.	.	.	4	.	2
Hypotrachyna afrorevoluta	.	.	.	.	.	.	.	.	.	.	86	.	13	5	.	.	.	.	.	.
Cladonia ochrochlora	.	.	.	.	.	.	.	.	.	.	57	.	.	.	.	.	.	.	.	.
Lepraria incana	13	.	.	.	.	20	.	.	.	.	71	50	.	18	7	.	.	.	33	4
Melanelixia subaurifera	.	.	.	.	.	.	.	.	.	12	43	50	13	9	7	.	.	.	.	.
Hypogymnia farinacea	.	.	.	.	.	.	.	.	.	.	.	100	13	5	7	.	.	.	.	.
Hypogymnia tubulosa	.	.	.	.	.	.	.	.	.	.	14	50	.	9	.	.	.	.	.	.
Bryoria implexa	.	.	.	.	.	.	.	.	.	.	.	50	.	.	.	.	.	.	.	.
Tuckermanopsis chlorophylla	.	.	.	.	.	.	.	.	.	.	14	50	.	5	.	.	.	.	.	.
Vulpicida pinastri	.	.	.	.	.	.	.	.	.	.	14	50	25	9	7	.	.	.	.	.
Menegazzia terebrata	.	.	.	3	.	.	.	.	.	.	.	.	63	.	.	.	.	7	.	16
Rinodina efflorescens	.	.	.	.	.	.	.	.	.	.	.	.	50	5	.	.	.	.	11	7
Megalaria pulverea	.	.	.	.	.	.	.	.	.	.	.	.	38	.	.	.	.	.	.	4
Lecanora cinereofusca	.	.	.	.	.	.	.	.	.	.	.	.	38	.	.	.	.	.	.	9
Menegazzia subsimilis	.	.	.	.	.	.	.	.	.	.	.	.	38	.	.	.	.	.	.	.
Biatora mendax	.	.	.	.	.	.	.	.	.	.	.	.	25	.	.	.	.	.	.	2
Lecanora substerilis	.	.	.	.	.	.	.	.	.	.	.	.	25	5	.	.	.	.	22	2
Lecanora intumescens	.	.	.	.	.	.	.	.	.	.	.	.	25	.	.	.	.	.	.	7
Usnea dasopoga	.	.	.	.	.	.	.	.	.	.	.	.	25	18	13	.	.	.	.	.
Violella fucata	.	.	.	.	.	.	.	.	.	.	.	.	25	23	.	.	.	.	11	9
Biatora helvola	.	.	.	.	.	.	.	.	.	.	.	.	25	.	.	.	.	.	.	.
Lepraria rigidula	6	.	.	.	.	.	.	.	.	.	.	.	25	.	.	.	.	.	.	.
Cladonia fimbriata	.	.	.	3	25	.	.	.	.	.	.	.	25	.	.	.	4	4	.	.
Rinodina subpariata	.	.	8	.	.	.	.	.	.	12	.	.	38	14	.	.	.	.	.	4
Scoliciosporum umbrinum	.	.	.	.	.	.	.	.	17	24	.	.	.	55	7	.	4	.	11	2
Melanohalea elegantula	.	.	.	.	.	.	.	.	17	.	.	.	.	41	20	.	.	.	.	.
Japewia aliphatica	.	.	.	.	.	.	.	.	17	.	.	.	.	25	.	.	.	.	.	.
Melanelixia glabra	.	.	.	.	.	.	.	.	.	.	.	.	.	.	33	.	2	.	.	2
Lecanora pulicaris	.	.	.	.	.	.	.	.	33	47	.	.	38	50	67	.	2	.	33	9

Cluster number (total 20)	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**
Code of cluster	**A**	**B1**	**B2**	**C**	**D**	**E1**	**E2**	**E3**	**E4**	**E5**	**F1**	**F2**	**F3**	**F4**	**F5**	**G1**	**G2**	**G3**	**G4**	**G5**
Number of relevés (total 293)	**16**	**12**	**12**	**31**	**4**	**5**	**3**	**2**	**6**	**17**	**7**	**2**	**8**	**22**	**15**	**3**	**51**	**27**	**9**	**45**
Ramalina farinacea	.	.	.	.	.	.	.	50	17	.	43	.	38	9	53	.	2	4	.	7
Physconia enteroxantha	.	.	.	.	.	.	.	.	17	.	.	.	.	.	40	33	.	.	.	.
**Waynea stoechadiana*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	100	.	.	.	.
Bacidia rubella	.	.	.	10	.	40	.	.	33	.	.	.	.	5	13	100	.	4	.	7
**Alyxoria culmigena*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	67	.	.	.	.
**Pannaria rubiginosa*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	67	.	.	.	.
**Coenogonium tavaresianum*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	67	.	.	.	.
Bacidina phacodes	6	.	8	.	.	.	.	.	.	.	.	.	13	.	.	67	.	.	.	7
**Hyperphyscia adglutinata*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	67	.	.	.	.
Alyxoria varia	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	67	2	15	.	11
Gyalecta flotowii	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	67	.	.	.	4
**Bactrospora dryina*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	33	.	.	.	.
**Cresponea premnea*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	33	.	.	.	.
**Piccolia ochrophora*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	33	.	.	.	.
**Pseudosagedia borreri*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	33	.	.	.	.
**Zamenhofia hibernica*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	33	.	.	.	.
**Nephroma laevigatum*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	33	.	.	.	.
Thelopsis rubella	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	33	.	.	.	2
**Pertusaria trochiscea*	.	.	.	.	.	.	.	.	.	.	14	.	.	.	.	33	.	.	.	.
Pertusaria hymenea	.	.	.	.	.	.	.	.	.	.	14	.	.	.	.	33	.	4	.	.
Pertusaria leioplaca	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	25	7	.	7
Opegrapha vulgata	.	8	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	44	.	.
Bacidina sulphurella	6	8	.	3	.	.	.	.	.	.	.	.	25	.	13	.	6	.	78	16
Micarea micrococca	.	.	.	.	.	.	.	.	.	.	.	.	13	.	.	.	.	.	33	2
Zwackhia viridis	.	17	.	.	.	.	.	.	.	.	.	.	13	5	.	.	2	7	11	38
Anisomeridium polypori	6	17	33	19	.	.	.	.	17	.	.	.	.	.	.	.	2	.	11	38
Biatora pontica	.	.	.	.	.	.	.	.	.	.	.	.	38	.	.	.	.	.	.	29
Diagnostic species of the class *Agonimietea repletae*																				
Agonimia repleta	50	33	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Diagnostic species of class *Neckeretea complanatae* (lichens)																				
Lobaria pulmonaria	.	.	.	10	75	100	.	.	17	.	.	.	13	5	60	.	.	4	.	7
Diagnostic species of the class *Physcietea*																				
Amandinea punctata	.	.	.	.	.	.	.	.	67	18	.	.	.	5	27	.	6	.	.	.
Myriolecis sambuci	.	.	.	.	.	.	.	.	83	.	.	.	.	9	33	.	.	.	.	.
Parmelina tiliacea	.	.	.	.	.	20	.	100	17	6	.	.	.	.	73	.	.	.	.	.
Physconia distorta	.	.	.	.	.	60	.	50	33	.	.	.	.	.	7	.	.	.	.	.
Phaeophyscia orbicularis	.	.	.	.	.	20	.	50	17	41	.	.	.	.	13	.	6	.	.	.
Parmelina pastillifera	.	.	.	.	.	.	.	.	33	.	.	.	.	41	13	.	.	.	.	.
Diagnostic species of class *Hypogymnietea physodes*																				
Hypogymnia physodes	.	.	.	.	.	20	.	.	.	6	71	100	25	41	53	.	6	63	.	.
Parmeliopsis ambigua	25	.	.	.	.	.	.	.	17	6	43	100	.	55	20	.	.	.	.	.
Platismatia glauca	.	.	.	.	.	.	.	.	17	.	14	50	50	64	60	.	.	19	.	2
Pseudevernia furfuracea	.	.	.	.	.	.	.	.	17	12	14	50	.	45	60	.	.	.	.	.
Diagnostic species of the class *Arthonio radiatae-Lecidelletea elaeochromae*																				
Graphis scripta	.	8	8	3	.	.	.	.	.	.	.	.	50	5	7	.	88	48	89	87
Pseudosagedia aenea	6	.	8	.	.	.	.	.	.	6	.	.	13	9	.	100	51	.	11	2
Pyrenula nitida	13	17	.	3	.	.	.	.	.	6	.	.	38	5	13	.	55	81	11	71
Thelotrema lepadinum	.	.	8	3	.	.	.	.	.	.	.	.	25	.	.	.	.	37	.	44
Lecanora argentata	.	.	.	.	.	.	.	.	17	41	14	.	63	59	67	.	29	22	11	49
Buellia disciformis	.	.	.	.	.	.	.	.	.	29	.	.	13	27	7	.	.	.	.	7
Lepra amara	.	.	.	.	.	.	.	.	33	6	43	50	100	45	87	.	2	52	11	18
Other species																				
**Phaeophyscia hirsuta*	.	.	.	.	.	40	.	.	.	.	.	.	.	.	.	33	.	.	.	.
Lecanora chlarotera	.	.	.	.	.	.	67	100	.	.	.	.	.	14	.	.	.	7	.	.
Phaeophyscia endophoenicea	.	.	.	.	.	.	.	.	67	.	.	.	.	9	40	.	4	.	.	2
Ramalina europaea	.	.	.	.	.	.	.	.	33	.	.	.	.	9	53	.	.	.	.	2
Parmelia submontana	.	.	.	.	.	.	.	.	33	.	.	.	.	5	33	.	.	.	.	.

Cluster number (total 20)	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Code of cluster	**A**	**B1**	**B2**	**C**	**D**	**E1**	**E2**	**E3**	**E4**	**E5**	**F1**	**F2**	**F3**	**F4**	**F5**	**G1**	**G2**	**G3**	**G4**	**G5**
Number of relevés (total 293)	**16**	**12**	**12**	**31**	**4**	**5**	**3**	**2**	**6**	**17**	**7**	**2**	**8**	**22**	**15**	**3**	**51**	**27**	**9**	**45**
Cladonia pyxidata	.	.	.	.	50	.	.	.	.	.	14	50	.	.	7	.	.	.	.	.
Biatora efflorescens	13	.	8	3	.	.	.	.	.	.	.	.	38	45	.	.	6	.	11	22
Cetrelia monachorum	.	.	.	.	.	.	.	.	.	.	.	.	38	.	47	.	.	.	.	9
Lecanora thysanophora	.	.	.	.	.	.	.	.	.	.	.	.	38	.	.	.	.	.	22	27
Fuscidea pusilla	.	.	.	.	.	.	.	.	.	.	.	.	.	27	.	.	.	.	33	.
Loxospora elatina	.	.	.	.	.	40	.	.	.	.	.	.	88	9	.	.	.	.	11	64
Lecania croatica	.	.	.	.	.	.	.	.	17	12	.	.	25	.	.	.	37	.	33	4
Candelariella efflorescens	31	.	.	.	.	.	.	.	50	59	.	.	.	32	13	.	4	.	22	.
Candelariella xanthostigma	.	.	.	.	.	.	100	.	100	29	.	.	.	18	40	.	2	.	.	.
Lepraria finkii	25	42	17	55	.	.	.	.	.	.	.	.	13	18	.	.	4	.	67	51
Buellia griseovirens	6	.	.	.	.	.	.	.	67	6	29	.	13	68	67	.	2	.	67	11
Parmelia saxatilis	.	.	.	3	.	.	.	.	50	.	71	.	50	64	100	.	.	19	.	7
Melanelixia glabratula	.	.	.	.	.	.	.	.	.	24	86	.	75	32	53	.	.	26	67	38
Parmelia sulcata	.	.	.	.	25	80	.	50	17	29	71	.	50	55	73	33	2	7	.	.
Phlyctis argena	.	8	.	.	.	.	.	.	50	29	57	50	100	64	87	.	27	59	67	87

Ordination

Based on the results of the NMDS ordination (Figure 3), the data can be divided into two groups. The first group (A–C) mainly includes relevés that are concentrated in the left part of the diagram and were sampled on the root system of the studied trees. By contrast, the second group (E–G) includes relevés made on the trunk and branches, which are concentrated in the right part of the ordination diagram. Cluster D, which does not include any relevé from the territory of Ukraine, is separated from the other two groups and is located in the lower part of the diagram. These results demonstrate that the units including communities formed in the basal part of trees are characterized by much more variable environmental conditions than those formed on the trunk and branches.

Characteristics of vegetation units

Cluster A (Tables 1, 2, Figures 3, 4, Suppl. material 1)

Synecology: Neutrophilous to moderately acidophilous, slightly nitrophilous, ombrophilous, hygrophilous, heliophilous epiphytic lichen communities on exposed roots and bases of old deciduous trees with smooth bark (e.g. *Fagus sylvatica*) near the subalpine belt (1150–1340 m a.s.l.).

Diagnostic species: *Agonimia repleta*, *Biatora chrysantha*, *B. radicicola*, *Caloplaca sorocarpa*, *Catinaria atropurpurea*, *Gyalideopsis helvetica*, *Lepraria jackii*, *Porpidia macrocarpa* (corticolous form).

Dominant species: *Biatora chrysantha*.

Constant species: *Agonimia repleta*, *Biatora chrysantha*, *B. radicicola*.

Synphysiognomy: Inconspicuous crustose lichen communities resembling a grey-greenish coating.

Synfloristics: Species-poor lichen communities. The lichens *Agonimia repleta*, *Biatora chrysantha*, *B. efflorescens*, *B. radicicola*, *Bacidia subincompta*, *Caloplaca sorocarpa*, *Catinaria atropurpurea*, *Frutidella furfuracea*, *Gyalideopsis helvetica*, *Rinodina orculata*, and *Verrucaria hegetschweileri* are rare species in the Carpathians.

Distribution: Beech habitats in the Carpathians polonynas.

Syntaxonomy: This cluster does not include any data from the literature. The new association *Biatoretum radicicolae* is proposed.

Subcluster B1 (Tables 1, 2, Figures 3, 4, Suppl. material 1)

Synecology: Neutrophilous, anitrophilous, ombrophilous, hygrophilous, moderately sciophilous epiphytic lichen communities on exposed roots and bases of deciduous trees with smooth bark (e.g. *Fagus sylvatica*) in the montane belt (500–1200 m a.s.l.).

Diagnostic species: *Agonimia repleta*, *Arthonia helvola*, *A. spadicea*, *Dictyocatenulata alba*.

Dominant species: *Dictyocatenulata alba*.

Constant species: *Arthonia helvola*, *Dictyocatenulata alba*, *Lepraria finkii*.

Synphysiognomy: Inconspicuous crustose lichen communities the color of roots and bark.

Synfloristics: Species-poor lichen communities. *Agonimia allobata*, *A. repleta*, *A. tristicula*, *Anisomeridim macrocarpum*, *Arthonia helvola*, *A. didyma*, *Cliostomum haematommatis*, *Dictyocatenulata alba*, *Biatora fallax*, *B. vernalis*, *Gyalecta herculina*, *Porina lectissima*, and *Strigula stigmatella* are rare species in the Carpathians.

Distribution: Carpathians (Central Europe).

Syntaxonomy: The new association *Dictyocatenulatetum albae* is proposed.

Subcluster B2 (Tables 1, 2, Figure 3, Suppl. material 1)

Synecology: Neutrophilous, anitrophilous, anombrophilous, hygrophilous, sciophilous, epiphytic lichen communities at the base of old trees with smooth bark (e.g. *Fagus sylvatica*) in the montane belt, 500–1200 m a.s.l.).

Table 2. Main phytosociological values of the epiphytic lichen communities on *Fagus sylvatica* of old-growth beech forests of western Ukraine and similar European communities (*= from literature only).

Cluster	Association	number releves	number species	Maximum species per releve	Minimum species per releve	Average species number	Average positive fidelity	Sharpness
A	*Biatoretum radicicolae*	16	32	14	2	6.50	18.81	82.76
B1	*Dictyocatenulatetum albae*	12	21	12	3	4.75	15.28	66.34
B2	Comm. *Gyalecta herculina*	12	19	9	3	4.08	18.92	67.44
C	*Biatoretum vernalis*	31	42	13	2	4.15	17.75	64.06
*D	*Nephrometum belli*	4	14	8	4	5.75	47.94	100.22
*E1	*Anaptychio ciliaris-Lobarietum pulmonariae*	5	24	13	9	11.00	36.81	83.28
*E2	*Lecanoretum carpinea montanum*	3	8	6	7	6.33	54.16	68.58
*E3	*Physcietum adscendentis* (incl. *Parmelietum trichotero-scorteae*)	2	22	13	11	12.00	38.14	70.00
E4	Derivative comm. *Physcia tenella* + *Parmelium saxatilis* + *Caloplaca sorocarpa*	6	75	31	7	20.67	21.45	69.03
E5	*Candelarietum concoloris*	17	52	18	5	9.82	15.08	78.73
*F1	*Pseudevernio furfuracea-Hypotrachynetum afrorevolutae*	7	27	14	7	10.71	19.27	40.63
*F2	*Parmelietum furfuraceae* (Incl. *Parmelietum physodo-sulcatae*)	2	16	11	8	9.50	29.27	49.40
F3	Derivative comm. *Platismatia glauca* + *Loxospora elatina*	8	67	35	8	19.25	20.03	61.06
F4	*Japewio aliphatici-Parmelietum saxatilis*	22	98	34	4	16.27	11.35	36.79
F5	*Parmelio tiliacei-Lobarietum pulmonariae*	15	83	31	6	19.60	12.38	39.40
*G1	*Hypocenomycetum stoechadianae*	3	25	18	7	12.67	52.76	104.20
G2	*Porinetum carpineae*	51	50	12	2	5.12	9.95	26.71
*G3	*Pertusarietum amarae* (incl. *Pyrenuletum nitidae*, *Thelotremetum lepadinii*, *Opegraphetum diaphorae*)	27	30	10	2	6.22	8.42	20.50
G4	*Buellio griseovirenti-Bacidinetum sulphurellae*	9	42	13	7	10.11	13.29	47.08
G5	*Thelotremo lepadini-Biatoretum ponticae*	45	92	25	4	10.93	8.34	29.78

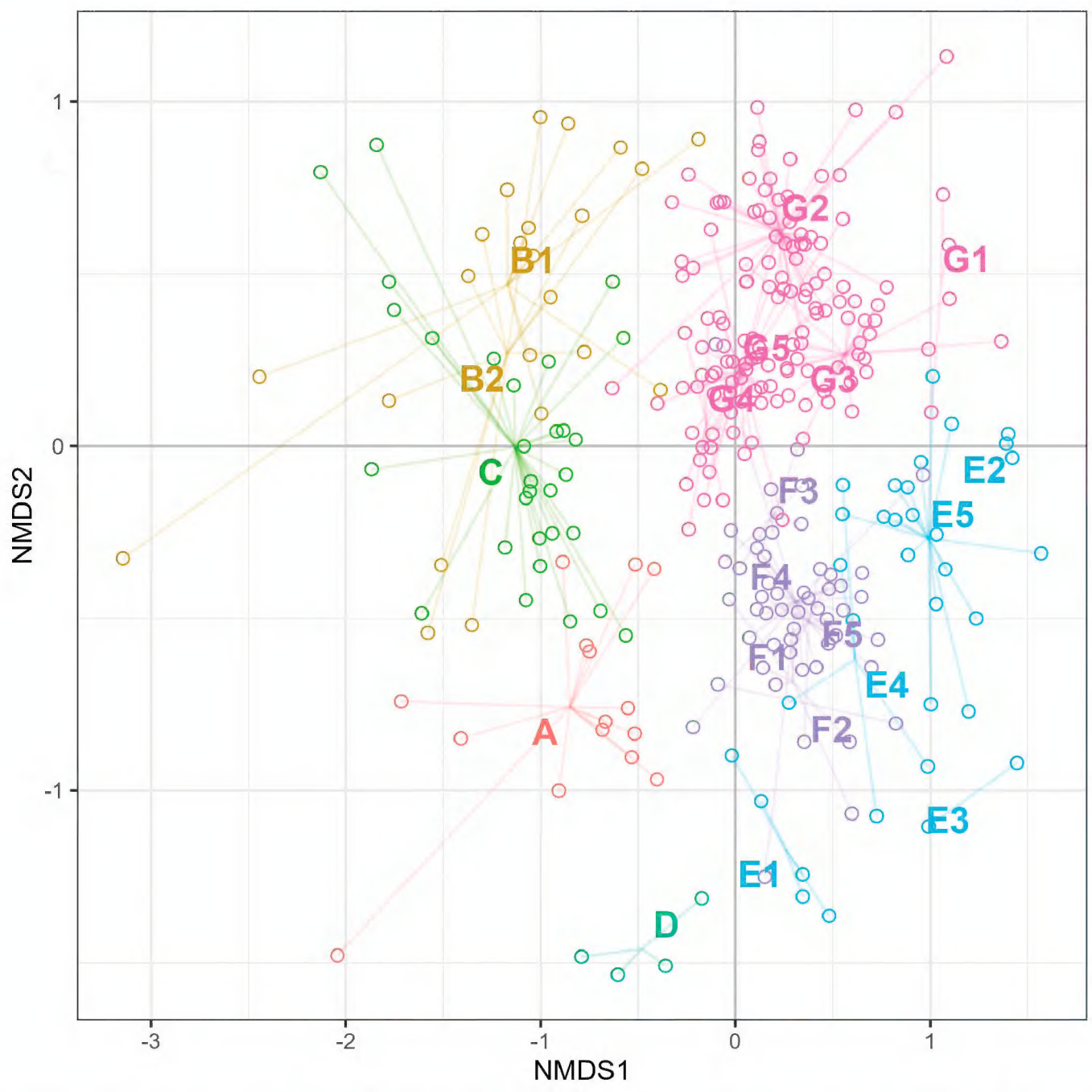

Figure 3. Non-metric multidimensional scaling (NMDS) of the epiphytic lichen communities from beech old-growth forests of western Ukraine and reference European communities. The unit codes label the centroids and correspond to those given in the text. The colors indicate the main groups. Stress of the model = 25.19793.

Diagnostic species: *Bacidia subincompta*, *Coenogonium pineti*, *Gyalecta herculina*, *Porina leptalea*.

Dominant species: Absent.

Constant species: *Bacidia subincompta*, *Coenogonium pineti*, *Porina leptalea*.

Synphysiognomy: Inconspicuous lichen communities with crustose lichens only.

Synfloristics: Species-poor lichen communities. The lichen *Gyalecta herculina* was included in the Red Data Book of Ukraine. *Arthonia didyma*, *Biatora vernalis*, *Micarea peliocarpa*, *Thelopsis rubella*, and *Zamenhofia pseudohibernica* are rare species.

Distribution: Primeval beech forest in the Carpathians.

Syntaxonomy: Needs future research (*Gyalecta herculina* comm.).

Cluster C (Tables 1, 2, Figure 3, Suppl. material 1)

Synecology: Mesophilous, anitrophilous, neutrophilous to moderately acidophilous, ombrophilous, hygrophilous, moderately sciophilous lichen communities with predominantly crustose lichens on the mosses of old trees with smooth bark (*e.g. Fagus sylvatica*) in the montane belt (500–1100 m a.s.l.).

Diagnostic species: *Biatora vernalis*, *Lepraria finkii*, *Strigula stigmatella*.

Dominant species: *Biatora chrysantha*, *Lepraria finkii*.

Constant species: *Biatora vernalis*, *Lepraria finkii*.

Synphysiognomy: Communities resembling dark to light greenish, dispersed crustose spots on mosses at the base of old deciduous trees (e.g. *Fagus sylvatica*) in the montane belt.

Synfloristics: Species-poor lichen communities. *Agonimia allobata*, *Biatora vernalis*, *Coenogonium luteum*, *Leptogium saturninum*, *Lobaria pulmonaria*, *Lopadium disciforme*, *Micarea botryoides*, *Mycobilimbia epixanthoides*, *Mycobilimbia carneoalbida*, *Nephroma parile*, *Normandina acroglypta*, *Pannaria conoplea*, *Parmeliella triptophylla*, *Peltigera degenii*, *Strigula stigmatella*, *Thelopsis rubella*, *Vezdaea aestivalis*, and *Zamenhofia pseudohybernica* are rare species.

Distribution: Known from old-growth beech forest in the Carpathians, rare in other forest habitats.

Syntaxonomy: The new association *Biatoretum vernalis-Striguletum stigmatellae* is proposed.

Cluster D (Tables 1, 2, Figure 3)

Synecology: This cluster aggregates lichen-bryophyte communities dominated by large foliose lichens growing on bryophytes on old trees (e.g. *Acer pseudoplatanus*, *Fagus sylvatica*) or, less commonly, on mossy rocks near the subalpine belt above 1100 m a.s.l. These communities are psychrophilous (at least in Central Europe), neutrophilous to slightly acidophilous, ombrophilous, hygrophilous, and moderately heliophilous.

Diagnostic lichen species: *Cetrelia cetrarioides*, *Cetrelia olivetorum*, *Cladonia pyxidata*, *Heterodermia speciosa*, *Lobaria pulmonaria*, *Nephroma bellum*, *N. resupinatum*, *Peltigera praetextata*, *Sticta fuliginosa*, *S. sylvatica*.

Constant lichen species: *Cetrelia olivetorum*, *Peltigera praetextata*, *Lobaria pulmonaria*, *Sticta fuliginosa*, *S. sylvatica*.

Dominant lichen species: *Lobaria pulmonaria*.

Synphysiognomy: Recognizable by the presence of large foliose lichens, such as the blackish *Sticta* and *Leptogium*, and large-lobed brown lichens such as *Lobaria pulmonaria* and *Nephroma* species. Occurs on moss cushions on trees, often in mountainous areas.

Synfloristics: These communities are lichen-poor, but include the rare European species *Lobaria pulmonaria*, *Nephroma bellum*, *Ricasolia amplissima*, *Sticta fuliginosa*, and *S. sylvatica*.

Distribution: Mountainous areas in Central Europe and oceanic areas in Western Europe.

Syntaxonomy: This cluster corresponds to the *Nephrometum belli* (alliance *Lobarion pulmonariae*, order *Antitrichietalia curtipendulae*, class *Neckeretea complanatae*). Communities of this cluster were not recorded during the fieldwork in western Ukraine.

Subcluster E1 (Tables 1, 2, Figure 3, Suppl. material 2)

Synecology: Mesophilous, moderately nitrophilous, neutrophilous, ombrophilous, heliophilous, epiphytic lichen communities on the bark of deciduous trees (*e.g. Fagus sylvatica*) in the lower montane belt in Asian Mts (250–600 m a.s.l.).

Figure 4. Communities of *Agonimietea repletae* class: a – exposed root systems in primeval beech forest (Zacharovanyi Krai-Velykyi Dil, UNESCO site), b – *Dictyocatenulatetum albae* on exposed root in shaded beech forest (Zacharovanyi Krai-Velykyi Dil, UNESCO site); c – *Biatoretum radicicolae* on exposed root in light beech forest near polonyna (Synevyr National Nature Park).

Diagnostic species: *Anaptychia ciliaris*, *Lobaria pulmonaria*, *Melanelixia subargentifera*, *Parainoa subconcolor*, *Parmelia sulcata*, *Phaeophyscia hirsuta*, *Physcia aipolia*, *Physconia detersa*, *P. distorta*, *P. perisidiosa*, *Rostania occultata*.

Dominant species: *Lobaria pulmonaria*.

Constant species: *Anaptychia ciliaris*, *Bacidia rubella*, *Lobaria pulmonaria*, *Loxospora elatina*, *Melanelixia subargentifera*, *Parainoa subconcolor*, *Parmelia sulcata*, *Phaeophyscia hirsuta*, *Physcia aipolia*, *Physconia detersa*, *Ph. distorta*, *Ph. perisidiosa*, *Rostania occultata*.

Synphysiognomy: These are communities with large lichens such as *Lobaria pulmonaria* intermixed with foliose physcioid lichens.

Synfloristics: This group includes moderately species-rich communities. *Rostania occultata*, *Phaeophyscia hirsuta*, *P. hispidula*, and *Parainoa subconcolor* are rare in Europe (Zhuravleva et al. 2004).

Distributions: Eastern Europe (Ural Mts).

Syntaxonomy: This cluster belongs to the association *Anaptychio ciliaris-Lobarietum pulmonariae* (Zhuravleva et al. 2004) and was not recorded during our field research.

Subcluster E2 (Tables 1, 2, Figure 3, Suppl. material 2)

Synecology: Moderately nitrophilous lichen communities with predominantly crustose species on the smooth bark of trees (Barkman 1958).

Diagnostic species: *Arthonia radiata*, *Caloplaca cerina*, *Candelariella xanthostigma*, *Lecanora carpinea* s. lat., *L. chlarotera*, *Lecidella elaeochroma*, *Rinodina polyspora*.

Dominant species: *Lecanora chlarotera*.

Constant species: *Arthonia radiata*, *Caloplaca cerina*, *Candelariella xanthostigma*, *Lecanora carpinea* s. lat., *L. chlarotera*, *Lecidella elaeochroma*.

Synphysiognomy: These communities comprise a mosaic of crustose lichens with a predominance of species of the genus *Lecanora* and other pioneer species, sometimes nitrophytic ones.

Synfloristics: Lichen-poor communities (Barkman 1958).

Distribution: Europe (Barkman 1958).

Syntaxonomy: This cluster belongs to the association *Lecanoretum carpinea montanum* (Barkman 1958). These communities don't occur in the old-growth beech forest of western Ukraine.

Subcluster E3 (Tables 1, 2, Figure 3, Suppl. material 2)

Synecology: Nitrophilous, mesophilous, heliophilous epiphytic lichen communities on the bark of deciduous trees (Ochsner 1928; Barkman 1958).

Diagnostic species: *Collema nigrescens*, *Flavoparmelia caperata*, *Hypotrachyna revoluta*, *Lecanora chlarotera*, *Lepra albescens*, *Leptogium saturninum*, *Parmelina tiliacea*, *Parmotrema perlatum*, *Physcia aipolia*, *Physconia distorta*, *Punctelia subrudecta*, *R. fastigiata*, *Xanthomendoza fulva*.

Dominant species: Absent.

Constant species: *Anaptychia ciliaris*, *Candelaria concolor*, *Collema nigrescens*, *Evernia prunastri*, *Flavoparmelia caperata*, *Hypotrachyna revoluta*, *Lecanora chlarotera*, *Lepra albescens*, *Leptogium saturninum*, *Parmelia sulcata*, *Parmelina tiliacea*, *Parmotrema perlatum*, *Phaeophyscia orbicularis*, *Physcia adscendens*, *Physcia aipolia*, *Physconia distorta*, *Punctelia subrudecta*, *Ramalina farinacea*, *R. fastigiata*, *Xanthomendoza fulva*, *Xanthoria parietina*.

Synphysiognomy: These communities include numerous physcioid and parmelioid lichens with a yellow-orange mosaic of xanthorioid lichens.

Synfloristics: Moderately species-rich lichen communities.

Distribution: Europe (Ochsner 1928; Barkman 1958).

Syntaxonomy: This cluster belongs to the association *Physcietum adsendentis* (Ochsner 1928) and *Parmelietum trichotero-scorteae* (Barkman 1958), and isn't recorded by our field research.

Subcluster E4 (Tables 1, 2, Figure 3, Suppl. material 2)

Synecology: Moderately nitrophilous, hygrophilous, neutrophilous to acidophilous, ombrophilous, heliophilous, epiphytic lichen communities on the bark of old deciduous trees with smooth bark and numerous fissures (e.g. *Fagus sylvatica*) near the subalpine belt (1100–1200 m a.s.l.).

Diagnostic species: *Amandinea punctata*, *Buellia griseovirens*, *Caloplaca turkuensis*, *Candelariella efflorescens*, *C. xanthostigma*, *Gyalecta fagicola*, *Lecanora saligna*, *Myriolecis sambuci*, *Parmelia submontana*, *Parmelina pastillifera*, *Pertusaria albescens*, *Phaeophyscia endophoenicea*, *Physcia tenella*, *Ramalina europaea*, *Rinodina griseosoralifera*, *Scoliciosporum chlorococcum*.

Constant species: *Amandinea punctata*, *Buellia griseovirens*, *Caloplaca turkuensis*, *Candelariella efflorescens*, *C. xanthostigma*, *Gyalecta fagicola*, *Lecanora saligna*, *Myriolecis sambuci*, *Parmelia saxatilis*, *P. submontana*, *Parmelina pastillifera*, *Pertusaria albescens*, *Phaeophyscia endophoenicea*, *Phlyctis argena*, *Physcia tenella*, *Ramalina europaea*, *Rinodina griseosoralifera*, *Scoliciosporum chlorococcum*.

Dominant species: Absent.

Synphysiognomy: Stands resemble a grayish crust composed of numerous crustose and foliose lichens on old beeches dispersed near the subalpine belt.

Synfloristics: These communities are lichen hotspots. *Bacidia vermifera*, *Caloplaca monacensis*, *Catillaria erysiboides*, *Gyalecta fagicola*, *Japewia aliphatica*, *Melanohalea elegantula*, *Mycoblastus affinis*, *Ochrolechia bahusiensis*, and *Rinodina capensis* are rare species.

Distribution: Carpathians (Central Europe).

Syntaxonomy: This is a derivative unranked community *Physcia tenella* + *Parmelium saxatilis* + *Caloplaca sorocarpa*, placed between the communities *Candelarietum concoloris* (subclaster E5), *Japewio aliphatici-Parmelietum saxatilis* (subcluster F4) and *Biatoretum radicicolae* (cluster A).

Subcluster E5 (Tables 1, 2, Figure 3, Suppl. material 2)

Synecology: Nitrophilous, hygrophilous to mesophilous, neutrophilous to slightly acidophilous, ombrophilous, heliophilous, epiphytic lichen communities on the bark of deciduous trees with smooth bark (e.g. *Fagus sylvatica*) in uplands and mountains (250–900 m a.s.l.).

Diagnostic species: *Buellia disciformis*, *Candelaria concolor*, *Candelariella efflorescens*, *Phaeophyscia orbicularis*, *Physcia stellaris*, *Scoliciosporum sarothamni*, *Xanthoria parietina*.

Dominant species: *Phlyctis argena*.

Constant species: *Buellia disciformis*, *Candelaria concolor*, *Candelariella efflorescens*, *Lecanora argentata*, *L. pulicaris*, *Lecidella elaeochroma*, *Phaeophyscia orbicularis*, *Physcia stellaris*, *Scoliciosporum sarothamni*, *Xanthoria parietina*.

Synphysiognomy: Resembles a grayish crust with a predominance of lichens of the *Physciaceae* family.

Synfloristics: Moderately species-rich lichen communities without rare lichens.

Distribution: Europe.

Syntaxonomy: These communities we included in the concept of the association *Candelarietum concoloris* (Gallé 1933, 1976).

Subcluster F1 (Tables 1, 2, Figure 3, Suppl. material 3)

Synecology: Slightly nitrophilous, acidophilous, heliophilous lichen communities on the bark of deciduous trees (mainly *Alnus glutinosa*, rare *Aesculus hippocastanum*, *Fagus sylvatica*, *Fraxinus excelsior*, *Rhamnus cathartica*) (Almborn 1948).

Diagnostic species: *Cladonia ochrochlora*, *Evernia prunastri*, *Hypogymnia physodes*, *Hypotrachyna afrorevoluta*, *Lepraria incana*, *Melanelixia glabratula*, *M. subaurifera*, *Parmelia saxatilis*.

Dominant species: *Hypogymnia physodes*, *Hypotrachyna afrorevoluta*, *Lepraria incana*.

Constant species: *Cladonia ochrochlora*, *Evernia prunastri*, *Hypogymnia physodes*, *Hypotrachyna afrorevoluta*, *Lepra amara*, *Lepraria incana*, *Melanelixia glabratula*, *M. subaurifera*, *Parmelia saxatilis*, *P. sulcata*, *Parmeliopsis ambigua*, *Phlyctis argena*, *Ramalina farinacea*.

Synphysiognomy: These communities include the characteristic foliose lichens *Hypotrachyna afrorevoluta* and *Hypogymnia physodes*.

Synfloristics: Moderately species-rich lichen communities (Barkman 1958).

Distribution: Carpathians (Central Europe).

Syntaxonomy: These communities belong to the *Pseudoevernio furfuracea-Hypotrachynetum afrorevolutae* (Almborn 1948; Barkman 1958; Delzenne et Gehu 1978), absent in western Ukraine.

Subcluster F2 (Tables 1, 2, Figure 3, Suppl. material 3)

Synecology: Anitrophilous, strongly acidophilous, photophilous, ombrophilous, strongly wind-resistant lichen communities on coniferous and deciduous trees with mainly rough bark (von Krusenstjerna 1945; Barkman 1958; Mucina et al. 2016).

Diagnostic species: *Bryoria implexa*, *Cladonia pyxidata*, *Hypogymnia tubulosa*, *H. farinacea*, *Hypogymnia physodes*, *Melanelixia subaurifera*, *Parmeliopsis ambigua*, *Tuckermannopsis chlorophylla*, *Vulpicida pinastri*.

Dominant species: *Hypogymnia physodes*, *Pseudevernia furfuracea*.

Constant species: *Bryoria implexa*, *Cladonia coniocraea*, *C. pyxidata*, *Evernia prunastri*, *Hypogymnia tubulosa*, *H. farinacea*, *Hypogymnia physodes*, *Lepra amara*, *Lepraria incana*, *Melanelixia subaurifera*, *Parmeliopsis ambigua*, *Platismatia glauca*, *Phlyctis argena*, *Pseudoevernia furfuracea*, *Tuckermannopsis chlorophylla*, *Vulpicida pinastri*.

Synphysiognomy: These communities include large portions of the grey diffuse overgrowth of fruticulose *Pseudoevernia furfuracea* and foliose *Hypogymnia physodes*.

Synfloristics: Moderately species-richness lichen communities (von Krusenstjerna 1945; Barkman 1958; Mucina et al. 2016).

Distribution: Carpathians (Central Europe).

Syntaxonomy: This cluster belongs to the association *Parmelietum furfuraceae* (Hilitzer 1925) which was not recorded on *Fagus sylvatica* in the study locations.

Subcluster F3 (Tables 1, 2, Figure 3, Suppl. material 3)

Synecology: Acidophilous to neutrophilous, anitrophilous, hygrophilous, moderately heliophilous to moderately sciophilous, ombrophilous, mesotermophilous, epiphytic lichen communities on deciduous trees with smooth bark (e.g. *Fagus sylvatica*) in the montane belt, often in mixed forest (with *Abies alba*, *F. sylvatica*, and *Picea abies*).

Diagnostic species: *Biatora efflorescens*, *B. helvola*, *B. mendax*, *Cetrelia monachorum*, *Cladonia fimbriata*, *Lecanora argentata*, *L. cinereofusca*, *L. intumescens*, *L. substerilis*, *L. thysanophora*, *Lepra amara*, *Lepraria rigidula*, *Loxospora elatina*, *Megalaria pulverea*, *Melanelixia glabratula*, *Menegazzia subsimilis*, *M. terebrata*, *Phlyctis argena*, *Rinodina efflorescens*, *R. subpariata*, *Usnea dasopoga*, *Violella fucata*.

Dominant species: Absent.

Constant species: *Graphis scripta*, *Lecanora argentata*, *Lepra amara*, *Loxospora elatina*, *Melanelixia glabratula*, *Menegazzia terebrata*, *Parmelia saxatilis* (incl. *P. ernstiae*), *Parmelia sulcata*, *Phlyctis argena*, *Platismatia glauca*, *Rinodina efflorescens*.

Synphysiognomy: A good diagnostic species combination is the presence of the foliose lichens *Cetralia cetrarioides* s. lat., *Menegazzia terebrata*, and *Menegazzia subsimilis* among a mosaic of crustose lichens.

Synfloristics: Species-rich communities in the Carpathians, with rare lichens such as *Arthonia didyma*, *Biatora helvola*, *B. mendax*, *B. pontica*, *Cetrelia cetrarioides* s. lat., *Hypogymnia vittata*, *Hypotrachyna afrorevoluta*, *Fuscidea cyathoides*, *Lecanora cinereofusca*, *L. substerilis*, *Lecidella subviridis*, *Lobaria pulmonaria*,

Megalaria pulverea, *Menegazzia subsimilis*, *Punctelia jeckeri*, *Rinodina efflorescens*, *R. excrescens*, and *R. subpariata*.

Distribution: Carpathians (Central Europe).

Syntaxonomy: This is a derivative community *Platismatia glauca* + *Loxospora elatina* between the associations *Japewio aliphatici-Parmelietum saxatilis* (subcluster F4) and *Thelotremo lepadini-Biatoretum ponticae* (subcluster G5).

Subcluster F4 (Tables 1, 2, Figures 3, 5, Suppl. material 3)

Synecology: Moderately acidophilous, slightly nitrophilous, hygrophilous, moderately heliophilous, ombrophilous, psychrophilous, epiphytic lichen communities on deciduous trees with smooth bark (e.g. *Fagus*) in the upper montane belt (above 1110 m a.s.l.).

Diagnostic species: *Biatora efflorescens*, *Buellia disciformis*, *B. griseovirens*, *Fuscidea pusilla*, *Japewia aliphatica*, *Melanohalea elegantula*, *Parmelia saxatilis*, *Parmelina pastillifera*, *Parmeliopsis ambigua*, *Platismatia glauca*, *Pseudevernia furfuracea*, *Scoliciosporum umbrinum*.

Constant species: *Lecidella elaeochroma*, *Melanelixia glabratula*, *Biatora efflorescens*, *Buellia disciformis*, *B. griseovirens*, *Fuscidea pusilla*, *Hypogymnia physodes*, *Japewia aliphatica*, *Lecanora argentata*, *Lecanora pulicaris*, *Lepra amara*, *Melanohalea elegantula*, *Parmelia saxatilis*, *P. sulcata*, *Parmelina pastillifera*, *Parmeliopsis ambigua*, *Phlyctis argena*, *Platismatia glauca*, *Pseudevernia furfuracea*, *Scoliciosporum umbrinum*.

Dominant species: *Parmelia saxatilis*, *Phlyctis argena*, *Platismatia glauca*, *Pseudevernia furfuracea*.

Synphysiognomy: Resembles a greyish crust with foliose and crustose lichens on old beeches near the subalpine belt.

Synfloristics: These communities are lichen hotspots. *Arthonia mediella*, *Bacidina egenula*, *Biatora ocelliformis*, *Cetraria cetrarioides*, *C. monachorum*, *Gyalecta flotowii*, *Hypotrachyna afrorevoluta*, *Japewia aliphatica*, *Lecanora substerilis*, *Lobaria pulmonaria*, *Melanohalea elegantula*, *Rinodina orculata*, and *Rinodina trevisanii* are rare species.

Distribution: Carpathians (Central Europe).

Syntaxonomy: We propose describing these communities as *Japewio aliphatici-Parmelietum saxatilis*.

Subcluster F5 (Tables 1, 2, Figures 3, 5, Suppl. material 3)

Synecology: Neutrophilous, moderately nitrophilous, hygrophilous, moderately heliophilous, ombrophilous, psychrophilous, epiphytic lichen communities on deciduous trees with smooth bark (e.g. *Fagus sylvatica*) in forests of the upper montane belt (above 1110 m a.s.l.).

Diagnostic species: *Buellia griseovirens*, *Cetrelia monachorum*, *Lecanora argentata*, *L. pulicaris*, *Lepra amara*, *Lobaria pulmonaria*, *Melanelixia glabra*, *Myriolecis sambuci*, *Parmelia saxatilis*, *P. submontana*, *P. sulcata*, *Parmelina tiliacea*, *Phaeophyscia endophoenicea*, *Phlyctis argena*, *Physconia enteroxantha*, *Platismatia glauca*, *Pseudevernia furfuracea*, *Ramalina europaea*, *R. farinacea*.

Constant species: *Buellia griseovirens*, *Candelariella xanthostigma*, *Cetrelia monachorum*, *Hypogymnia physodes*, *Lecanora argentata*, *L. pulicaris*, *Lecidella elaeochroma*, *Lepra amara*, *Lobaria pulmonaria*, *Melanelixia glabratula*, *Parmelia saxatilis*, *P. sulcata*, *Parmelina tiliacea*, *Phaeophyscia endophoenicea*, *Phlyctis argena*, *Physconia enteroxantha*, *Platismatia glauca*, *Pseudevernia furfuracea*, *Ramalina europaea*, *R. farinacea*.

Dominant species: *Parmelia saxatilis*, *Parmelia sulcata*, *Pseudevernia furfuracea*.

Synphysiognomy: These communities host numerous greyish foliose parmelioid lichens (*Parmelia*, *Parmelina*, *Cetrelia*) with spots of *Lobaria pulmonaria*, lichens with large brown lobes.

Synfloristics: Species-rich lichen communities. *Caloplaca turkuensis*, *Cetrelia cetrarioides*, *Cetrelia monachorum*, *Cetrelia olivertorum*, *Collema nigrescens*, *Heterodermia speciosa*, *Gyalecta fagicola*, *Lecanora expersa*, *Lobaria pulmonaria*, *Melanohalea elegantula*, *Pertusaria alpina*, *Ochrolechia alboflavescens*, and *Rinodina trevisanii* are rare species.

Distribution: Carpathians (Central Europe).

Syntaxonomy: We propose describing these communities as *Parmelio tiliacei-Lobarietum pulmonariae*.

Subcluster G1 (Tables 1, 2, Figure 3, Suppl. material 4)

Synecology: Thermophilous, neutrophilous, moderately nitrophilous, sciophilous, epiphytic, mainly crustose lichen communities on the neutral to moderately acidic, porose bark of old trees (e.g. *Quercus*) in shaded, humid habitats (Abbassi-Maaf et Roux 1987; Mucina et al. 2016).

Diagnostic species: *Alyxoria culmigena*, *Alyxoria varia*, *Bacidia rubella*, *Bacidina phacodes*, *Bactrospora dryina*, *Coenogonium tavaresianum*, *Cresponea premnea*, *Gyalecta flotowii*, *Hyperphyscia adglutinata*, *Nephroma laevigatum*, *Pannaria rubiginosa*, *Phaeophyscia hirsuta*, *Piccolia ochrophora*, *Pseudosagedia aenea*, *P. borreri*, *Thelopsis rubella*, *Waynea stoechadiana*, *Zamenhofia hibernica*.

Constant species: *Alyxoria culmigena*, *Alyxoria varia*, *Bacidia rubella*, *Bacidina phacodes*, *Coenogonium tavaresianum*, *Gyalecta flotowii*, *Hyperphyscia adglutinata*, *Pannaria rubiginosa*, *Pseudosagedia aenea*, *Waynea stoechadiana*.

Dominant species: *Bacidia rubella*, *Bacidina phacodes*, *Pannaria rubiginosa*.

Synphysiognomy, synfloristics: See Abbassi-Maaf et Roux (1987).

Distribution: Mediteranean (France). It is not found in western Ukraine.

Syntaxonomy: This cluster belongs to the association *Hypocenomycetum stoechadianae* Abbassi Maaf et Roux 1987.

Subcluster G2 (Tables 1, 2, Figures 3, 6, Suppl. material 4)

Synecology: Moderately acidophilous, anitrophilous, sciophilous, mesophilous, mesothermophilous, epiphytic crustose lichen communities on trees with smooth bark (e.g. *Fagus sylvatica*) in shaded and moderately humid habitats.

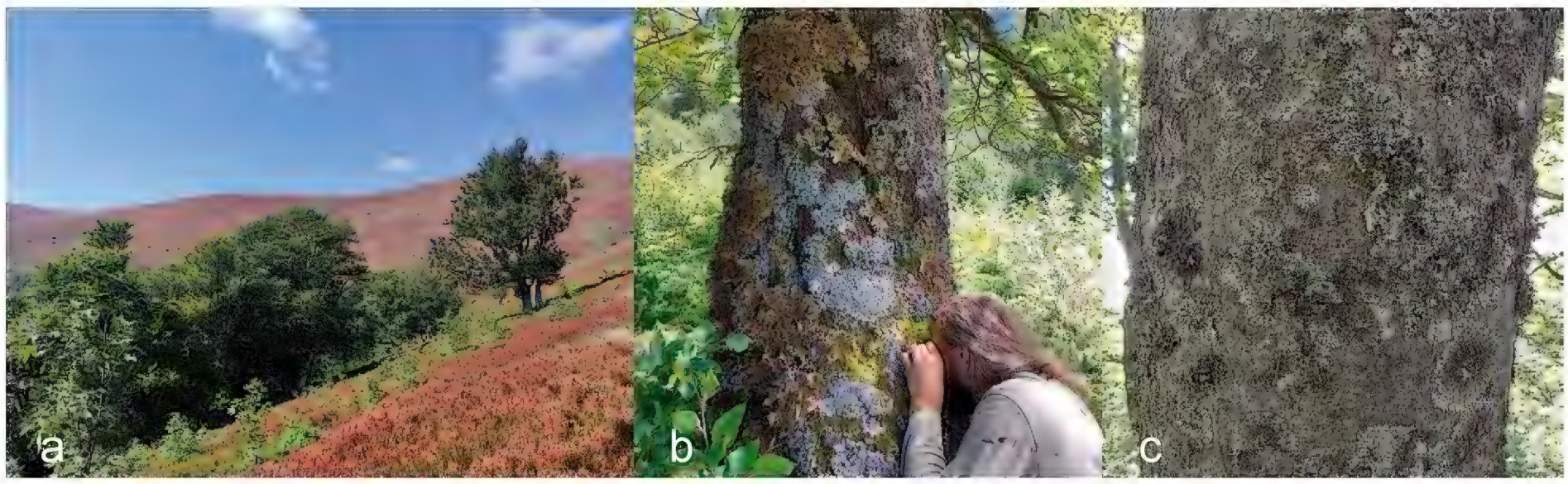

Figure 5. Communities of *Hypogymnietea physodis*: a – timberline beech forest with communities of the class; b – old beech trunk cover by *Parmelio tiliacei-Lobarietum pulmonariae*; c – old beech trunk cover by *Japewio aliphatici-Parmelietum saxatilis*.

Diagnostic species: *Graphis scripta*, *Lecania croatica*, *Pertusaria leioplaca*, *Pseudosagedia aenea*.

Constant species: *Graphis scripta*, *Lecania croatica*, *Pertusaria leioplaca*, *Pyrenula nitida*, *Pseudosagedia aenea*.

Dominant species: *Biatora efflorescens*, *Graphis scripta*, *Lecania croatica*, *Phlyctis argena*, *Pseudosagedia aenea*, *Pyrenula nitida*.

Synphysiognomy: These communities form a mosaic of crustose lichens with conspicuous whitish spots of *Phlyctis argena* and *Pertusaria leioplaca*, as well as perithecioid lichens with dark thalli such as *Pyrenula nitida* and *Pseudosagedia aenea*.

Synfloristics: Lichen-poor communities.

Distribution: Europe, including the Carpathians and allied uplands in Ukraine.

Syntaxonomy: This cluster belongs to the *Porinetum carpineae* Barkman 1958, because the holotype with four relevés from the OD of this association fall into this cluster.

Subcluster G3 (Tables 1, 2, Figure 3, Suppl. material 4)

Synecology: These are a complex of similar anitrophilous, mesophilous, neutrophilous to moderately acidophilous epiphytic lichen communities on trees with smooth bark (e.g. *Fagus*) (Hilitzer 1925; Barkman 1958).

Diagnostic species: *Hypogymnia physodes*, *Opegrapha vulgata*, *Pyrenula nitida*, *Thelotrema lepadinum*.

Constant species: *Hypogymnia physodes*, *Graphis scripta*, *Lepra amara*, *Opegrapha vulgata*, *Phlyctis argena*, *Pyrenula nitida*.

Dominant species: *Alyxoria varia*, *Graphis scripta*, *Lepra amara*, *Phlyctis argena*, *Pyrenula nitida*, *Thelotrema lepadinum*.

Synphysiognomy: These communities form a dispersed mosaic of crustose lichens with visible but fine, light spots of *Phlyctis argena*, *Pertusaria amara*, *Thelotrema lepadinum*, and *Graphis scripta* with hieroglyph-like apothecia.

Synfloristics: Moderately species-rich lichen communities (Barkman 1958).

Distribution: Central and Northern Europe (Barkman 1958).

Syntaxonomy: This cluster belongs to the associations *Pertusarietum amarae*, *Pyrenuletum nitidae*, *Thelotremetum lepadinii* of Hilitzer (1925), and *Opegraphetum diaphorae* Barkman 1958. This cluster includes 28 relevés from the type dataset, including the type relevé from Hilitzer (1925), but no records from western Ukraine.

Subcluster G4 (Tables 1, 2, Figure 3, Suppl. material 4)

Synecology: Moderately acidophilous and sciophilous, slightly nitrophilous, mesophilous, ombrophilous, mesothermophilous, epiphytic lichen communities on the smooth bark of young (30–60 year) deciduous trees (e.g. *Fagus sylvatica*) in the montane belt (300–900 m a.s.l.).

Diagnostic species: *Bacidina sulphurella*, *Buellia griseovirens*, *Fuscidea pusilla*, *Graphis scripta*, *Lecania croatica*, *Lepraria finkii*, *Melanelixia glabratula*, *Micarea micrococca*.

Constant species: *Bacidina sulphurella*, *Buellia griseovirens*, *Graphis scripta*, *Lepraria finkii*, *Melanelixia glabratula*, *Phlyctis argena*.

Dominant species: *Graphis scripta*, *Phlyctis argena*.

Synphysiognomy: Appears as crusty greenish-grey spots on the smooth bark of young trees.

Synfloristics: Moderately species-rich communities. *Biatora ocelliformis*, *Lecanora subcarpinea*, *L. substerilis*, *Lopadium disciforme*, *Rinodina effloresens*, and *Pertusaria pupillaris* are rare species.

Distribution: Carpathians (Central Europe).

Syntaxonomy: We describe this cluster here as *Buellio griseovirenti-Bacidinetum sulphurellae*.

Subcluster G5 (Tables 1, 2, Figure 3, Suppl. material 4)

Synecology: Neutrophilous to slightly acidophilous, anitrophilous, hygrophilous, moderately sciophilous, mesothermophilous, epiphytic lichen communities on the smooth bark of old deciduous trees (e.g. *Fagus sylvatica*) in the montane belt (300–900 m a.s.l.).

Diagnostic species: *Anisomeridium polypori*, *Biatora pontica*, *Graphis scripta*, *Lecanora thysanophora*, *Loxospora elatina* s. lat. (incl. *Chicitaea cristinae*), *Phlyctis argena*, *Pyrenula nitida*, *Thelotrema lepadinum*, *Zwackhia viridis*.

Figure 6. Communities of *Arthonio radiatae-Lecidelletea elaeochromae*: a – primeval beech forest with trees cover by *Thelotremeto lepadini-Biatoretum ponticae* (Zacharovanyi Krai-Velykyi Dil, UNESCO site); b – old beech trunk cover by *Thelotremeto lepadini-Biatoretum ponticae* (Zacharovanyi Krai-Velykyi Dil, UNESCO site); c – old beech trunk cover by *Porinetum carpineae* (Khotyn upland); d – young beech trunk cover by *Buellio griseovirenti-Bacidinetum sulphurellae* (Zacharovanyi Kray National Nature Park).

Constant species: *Graphis scripta*, *Lecanora argentata*, *Lepraria finkii*, *Loxospora elatina* s. lat. (incl. *Chicitaea cristinae*), *Phlyctis argena*, *Pyrenula nitida*, *Thelotrema lepadinum*.

Dominant species: *Graphis scripta*, *Phlyctis argena*, *Pyrenula nitida*, *Thelotrema lepadinum*.

Synphysiognomy: These communities form a crustose, predominantly light grey, sorediate mosaic on old beech trunks, with unusual foliose lichens (e.g. *Menegazzia terebrata* and *Cetrelia monachorum*).

Synfloristics: These communities are lichen hotspots. *Arthonia didyma*, *Bacidina phacodes*, *Biatora efflorescens*, *B. meiocarpa*, *B. mendax*, *B. pontica*, *B. vernalis*, *Biatoridium monasteriense*, *Chicitaea cristinae*, *Catinaria atropurpurea*, *Cetrelia monachorum*, *Gyalecta flotowii*, *Lecanora substerilis*, *Lecidella subviridis*, *Lobaria pulmonaria*, *Lopadium disciforme*, *Loxospora cismonica*, *Megalaria laureri*, *M. pulverea*, *Parmeliella triptophylla*, *Pseudosagedia byssophila*, *Pyrenula laevigata*, *Rinodina subpariata*, *Schismatomma pericleum*, *Thelocarpon intermediellum*, *Thelopsis rubella*, *Strigula stigmatella*, and *Zamenhofia pseudohibernica* are rare species.

Distribution: Carpathians (Central Europe).

Syntaxonomy: We propose the new association *Thelotremo lepadini-Biatoretum ponticae* for these communities.

Discussion

Diversity of lichen communities on *Fagus sylvatica* in western Ukraine

Despite the significant species diversity of epiphytic lichens on the bark of *Fagus sylvatica* in the beech forests of western Ukraine, the diversity at community level was limited to only 12 lower-rank units. The poorest lichen communities were found in old-growth beech forests in the Khotyn and western Podillia uplands, as well as in Roztochchia. Only two species-poor associations, *Porinetum carpineae* and *Candelarietum concoloris*, were revealed there. In the Khotyn uplands, the *Porinetum carpineae*, as well as beech forests, are situated at the easternmost limit of their distribution in Ukraine. Interestingly, this association develops only on young beeches in the Carpathians, but it was also found on 250-year-old trees in the uplands.

Epiphytic communities in the old-growth beech forests of the Ukrainian Carpathians are more diverse. The association *Thelotremo lepadini-Biatoretum ponticae* (class *Arthonio radiatae-Lecidelletea elaeochromae*) is confined to the trunks of old-growth beeches in primeval forests of the Carpathians. These communities are species rich and have a significant number of rare European species. Lichen species which are mainly considered indicators of the ecological integrity of forest habitat are associated with it. A rare and unique sciophilic association, *Dictyocatenulatum albae*, was found on the bare roots of beeches or at the base of the trunk in primeval beech forest. Drastic changes in ecological conditions near the timberline are also reflected in the sudden shift of epiphytic communities from the *Arthonio radiatae-Lecidelletea elaeochromae* class, which mainly grows in forest on slopes, to the *Hypogymnietea physodis* class, which appears in a narrow strip of beech forest (approximately 100 meters wide) in front of polonynas. The *Japewio aliphatici-Parmelietum saxatilis* and *Parmelio tiliacei-Lobarietum pulmonariae* associations of the last class are responsible for the record levels of species diversity of epiphytic lichens in Central Europe (Vondrák et al. 2018). In addition, the heliophilous association *Biatorietum radicicolae* on the bare roots of beeches at the timberline is unique and rare in the Ukrainian Carpathians. It should be noted that the beech forests of the Ukrainian Carpathians are typically not a habitat of nitrophilous communities of the *Physcietea* class. However, the presence of these epiphytic communities in old-growth forests, including UNESCO forests in Ukraine's plains, indicates significant eutrophication of these habitats.

We did not find any correlation between epiphytic lichen communities on beeches and EUNIS units for the three types of beech forests (T17, T18 and T32). Probably, certain patterns can be identified when studying epiphytic lichen communities of all woody species present in these habitats.

Lichen communities as indicators of state of old-growth forest

Epiphytic lichen communities can serve as indicators for identifying natural beech forests, quasi-primeval forests, and primeval forests. The lichen communities of the *Thelotremo lepadini-Biatoretum ponticae* (*Graphidion scriptae* alliance) are strongly correlated with typical recognized primeval forests. These communities are most commonly found on the bark of old *Fagus sylvatica* trunks in the Shyrokyi Luh massif of the Carpathian Biosphere Reserve, which is included in the UNESCO World Natural Heritage site. In our opinion, these communities can be used as indicator communities for primeval beech forest. The species-poor *Dictyocatenulatetum albae*, which is most common in the primeval beech forests of Zacharovanyi Krai National Nature Park, can also be considered an indicator community. It includes a notable set of indicator species such as *Arthonia helvola*, *Anisomeridium macrocarpum*, *Dictyocatenulata alba*, and *Gyalecta herculina*.

The development of lichen communities on mosses is considered one of the indicators of the climax stage of old-growth forest development (Schubert and Stordeur 2011). Lichen species of the *Lobarion pulmonariae* alliance are well-known indicators of the ecological integrity of forest ecosystems. These communities have not yet been recorded in the Ukrainian Carpathians. It is hypothesised that such psychrophilic communities are declining rapidly in the Carpathians due to global climate change. However, the *Biatoretum vernalis* may represent a vicariant community on mosses in primeval forests. These mesothermophilic communities host recognized indicators of the ecological integrity of forest habitats, including crustose lichens such as *Biatora vernalis*, *Mycobilimbia carneoalbida*, *Parmeliella triptophylla*, *Strigula stigmatella*, and *Zamenhofia pseudohibernica*.

The impacts of moderate grazing have contributed to the formation of ecotone forest habitats near the timberline. As a result, species-rich communities of the alliance *Parmelion physodis* and its derivative communities of *Xanthorion parietinae* have developed on the bark of trees in old-growth beech forest at locations such as Menchul, Kuk, Borzhava, and Krasna polonynas. However, the high species richness of lichen communities associated with *Parmelion physodis* in old-growth beech forest near treeline does not align with classic primeval beech forests on mountain slopes. Nevertheless, these old-growth forests and quasi-primeval forests host the highest number of rare lichens within the *Japewio aliphatici-Parmelietum saxatilis* and *Parmelio tiliacei-Lobarietum pulmonariae*. The reduction of economic activity in polonynas, particularly the significant decrease in sheep grazing, has led to an increase in *Fagus sylvatica* and *Acer pseudoplatanus* in the understorey gaps between old *F. sylvatica* trees (Khodosovtsev et al. 2024). In these dense, dark thickets in the understorey, heliophilous epiphytic communities on old beeches become impoverished or disappear entirely. Species like *Heterodermia speciosa*, *Collema nigrescens*, *Melanelixia elegantula*, and *Varicellaria hemispherica* are no longer present in such poor communities,

and *Biatorion radicicolae* communities are completely absent (e.g. in the beech forest near the Kuk polonyna). Conversely, intensive management in the ecotone between beech forests and mountain grasslands results in nitrification of the bark on old trees, facilitating the formation of nitrophilic associations of the *Xanthorion parietinae* alliance. Nitrophilic communities of the *Candelarietum concoloris* lack indicator lichen species of the ecological inegrity of forest habitats and rare lichen species (e.g. as observed in the communities on Bozna Mountain). This community is often associated with human activity, such as close proximity to settlements, vegetable gardens, and areas for animal grazing, as well as fortifications from the First World War (near the old-growth beech forest of the Bozna Mts).

Epiphitic lichen communities as potential hotspots

A certain number of the analyzed plots exhibit similarities with multiple clusters. We consider them derivative (transitional) communities between different classes. There are two such derivative communities: Clusters E3 and F4, with average species richness of about 20 per relevé.

Cluster F4 (*Physcia tenella* + *Parmelia saxatilis* + *Caloplaca sorocarpa*-derivative community) develops on old *Fagus sylvatica* trees in the ecotone zone between beech forest and polonyna, at elevations of 1100–1200 m a.s.l. The trees hosting these communities are often crooked, with exposed roots, patches of smooth bark, and cracks. These areas exhibit varying degrees of mineral encrustation on the bark resulting from the weathering of bedrock in the nearby mountain pastures and subsequent penetration into the upper layers of the periderm. Encrustation can significantly alter the acidity of *F. sylvatica* bark. It is well-known that the pH of *F. sylvatica* bark ranges from 4.1 to 7.1 (Barkman 1958). Moderate human activity, particularly sheep farming, locally increases nitrification in mountain pastures (*polonynas*). These factors influence species composition of *Hypogymnietea physodis*, *Physcietea*, and their derivative communities. The average number of species in these derivative communities is the highest, reaching 20.6 species per relevé for Cluster E4 (Table 2). In total, we recorded 75 species of lichens across six relevés. The reason for this is probably a certain overlapping of conditions and, accordingly, species composition of three different classes of lichen vegetation. Among the diagnostic species of the *Physcietea adscendentis* class, we identified *Amandinea punctata*, *Physcia adscendens*, *P. tenella*, *Physconia distorta*, *P. perisidiosa*, and *Xanthoria parietina*. The species *Pseudevernia furfuracea*, *Platismatia glauca*, and *Parmeliopsis ambigua* are diagnostic for the class *Hypogymnietea physodis*, while *Caloplaca sorocarpa* and *Rinodina orculata* are diagnostic for *Agonimietea repletae*. We documented such communities in the Menchul, Kuk, and Borzhava polonynas of the Transcarpathian region.

Species-rich derivative communities are occasionally formed in beech forests on the slopes of the Carpathians within the middle forest zone (Cluster F3). These communities can be observed in mixed forests, particularly where *Abies alba* and *Picea abies* occur in stands alongside light old-growth beech forests. These communities exhibit high species richness, e.g. Cluster F3 with 67 species recorded across eight relevés (Table 2). These epiphytic communities are characterized by diagnostic species of the predominantly neutrophilic class *Arthonio radiatae-Lecidelletea elaeochromae*, such as *Graphis scripta*, *Phlyctis argena*, *Pyrenula nitida*, and *Thelotrema lepadinum*. They also include diagnostic species of the predominantly acidophilic class *Hypogymnietea physodis*, such as *Platismatia glauca*, *Pseudevernia furfuracea*, *Hypogymnia physodis*, and *Vulpicida pinastri*. Such communities have been recorded in the Gorgany Nature Reserve, Zacharovany Krai National Nature Park, and less frequently in the Carpathian Biosphere Reserve (Shyrokyi Luh massif).

It is likely that such derivative communities form the basis of lichen hotspots in the beech forests of the Carpathians (Vondrák et al. 2018; Malíček et al. 2018). These communities are quite rare, occurring on a small number of tree species and coexisting within 1-hectare plots alongside other typical associations. For example, on the polonyna Menchul, in addition to the derivative community *Physcia tenella* + *Parmelia saxatilis* + *Caloplaca sorocarpa* (1 relevé), the following communities were recorded: *Parmelieto pastilliferi-Scoliciosporetum umbrinae* (10 relevés), *Parmelio tiliacei-Lobarietum pulmonariae* (1 relevé), and *Biatoretum radicicolae* (8 relevés). In Gorgany Nature Reserve, the derivative community *Platismatia glauca* + *Loxospora elatina* s. l. (4 relevés) was identified, along with *Parmelieto pastilliferi-Scoliciosporetum umbrinae* (1 relevé on a beech branch), *Porinetum carpineae* (2 relevés), *Buellio griseovirenti-Bacidinetum sulphurellae* (1 relevé), and *Thelotremo lepadini-Biatoretum ponticae* (6 relevés) on *Fagus sylvatica*.

Beech forest areas with derivative communities require special attention and management due to the high concentration of species considered indicators of the ecological integrity of old-growth communities, as well as species requiring protection at various levels, all within relatively small spatial scales.

Comparison with similar European communities

Clusters A and B – communities on exposed roots and bases of trunks (*Agonimietea repletae*)

In the old-growth beech forests on the slopes of the Carpathians, inconspicuous lichen communities grow on the roots or at the base of old trees. For a long time, these communities remained poorly studied and largely overlooked. However, in the last quarter-century, new species such as *Agonimia repleta* (Czarnota and Coppins 2008), *Biatora radicicola* (Printzen et al. 2016), and *Verrucaria viridigrana* (Breuss 1998) have been described in these microhabitats. In addition to these specific taxa, distinct species-poor and rare communities are also formed in these habitats.

The most intriguing lichen communities develop on the exposed roots of old beeches near the upper forest line in so-called near-polonyna landscapes (Cluster A). Under these conditions, specific inconspicuous communities

with characteristic species such as *Biatora radicicola*, *Caloplaca sorocarpa*, *Rinodina orculata*, *Tetramelas chloroleuca*, and *Verrucaria hegetschweileri* are formed. Currently, none of the previously described lichen associations are directly related to these communities.

It was important for us to analyze the relationship of our relevés, particularly those made on the roots and bases of *Fagus sylvatica*, to the *Hypocenomycetum stoechadianae* association known from the Mediterranean. This association develops at the base of old trees with porous bark, and is part of the distinct *Agonimion octosporae* alliance (Bültmann et al. 2015; Mucina et al. 2016). However, diagnostic species of the *Agonimion octosporae* alliance, such as *Bacidia rubella*, *Bacidina phacodes*, *Biatoridium monasteriense*, *Coenogonium luteum*, and *Thelopsis rubella*, have very low frequency and fidelity in various clusters and subclusters (B1, B2, C, E1, E4, F3, G5) of the total dataset (Table 2). Phytosociological analysis revealed its proximity to *Graphidion scriptae* and its unique position within *Arthonio radiatae-Lecidelletea elaeochromae* (cluster G1, Figure 3). These findings support the idea of distinguishing a separate order, *Bacidinetalia phacodis*, for such communities (Bültmann et al. 2015; Mucina et al. 2016). Due to their distinct species composition, ecological characteristics, and chorological features, these communities could even be considered part of a separate class in the future.

Considering its clear ecological affinity and distinct set of characteristic species, we propose classifying this community as a separate alliance: *Biatorion radicicolae*, with a single association, *Biatorietum radicicolae*. In addition to the characteristic species, the differential species for this association include *Gyalideopsis helvetica* and *Frutidella furfuracea*. These communities also host lichens that are typically saxicolous species growing on silicate rocks, such as *Aspicilia laevata*, *Porpidia crustulata*, and *Porpidia macrocarpa*.

Subcluster B1 comprises rare lichen communities that develop in moderately sciophilous conditions on the roots of old beeches in the middle forest belt. These communities are characterized by a number of diagnostic species, including *Agonimia repleta*, *Arthonia helvola*, and *Dictyocatenulata alba*. A closely related community in terms of ecological preferences is a species-poor community dominated by *Gyalecta herculina* (subcluster B2). This lichen is a sciophyte that predominantly grows monodominantly in rain-protected depressions between the root systems of old *Fagus sylvatica* trees. These species may well be considered characteristic of the proposed new alliance *Dictyocatenulation albae*. The community with *Gyalecta herculina* (subcluster B2) is represented by few relevés and requires further investigation.

Considering the distinct ecological specialization of communities associated with the root systems and the bases of the trunks of old deciduous trees with smooth bark (primarily *Fagus sylvatica*), as well as the presence of characteristic species from two alliances, we propose classifying these communities as a separate order: *Agonimietalia repletae*. The characteristic species of this order may include those shared by both alliances, particularly *Agonimia repleta*, *Biatora chrysantha*, *Gyalecta herculina*, etc. The presence of a sufficient number of diagnostic and character species (see chapter 'New syntaxa and lectotypification') justifies the inclusion of all these communities within a new class: *Agonimietea repletae*.

Clusters C and D – communities on mosses (*Lobarion pulmonariae* and *Biatorion vernalis*)

Only the lectotype of the *Nephrometum belli* association, along with three relevés of the OD, were contained within cluster D, which we consider an association within the *Lobarion pulmonariae* alliance. Discussions about the placement of *Lobarion pulmonariae* associations in the system of lichen-bryophyte syntaxa have been ongoing for decades (Klement 1955; Barkman 1958; Wirth 1968; James et al. 1977; Schubert and Stordeur 2011). *Lobarion pulmonariae* is often broadly interpreted to include all communities where *Lobaria pulmonaria* occurs (Gauslaa 1995; Kondratyuk et al. 1997). Less frequently, it encompasses epiphytic lichens that are not typically found on bryophytes but which occur within the sampling relevé area, such as *Arthonia didyma*, *Acrocordia gemmata*, *Pertusaria pertusa*, and *Pertusaria hymenea*, (James et al. 1977). In the original description by Hilitzer (1925), the typical community of *Lobarion pulmonariae* is species-poor and represented in five relevés. Alongside bryophytes, it includes *Cetrelia cetrarioides*, *C. olivetorum*, *Lobaria pulmonaria*, *Parmelia sulcata*, *Nephroma resupinatum*, *N. bellum*, *Heterodermia speciosa*, *Peltigera praetextata*, *Sticta sylvatica*, and *Sticta fuliginosa*. Additionally, fruticose species such as *Cladonia pyxidata* and *Cladonia fimbriata*, as well as one crustose species, *Mycobilimbia carneoalbida*, are found growing on bryophyte beds. The differential species include *Lobaria pulmonaria*, *Peltigera praetextata*, *Sticta sylvatica*, and *Sticta fuliginosa*. The last two species are most likely characteristic species of the association. Despite significant interest in this community from European scientists as an indicator of the ecological integrity of forest habitats, there are relatively few published relevés of these or similar associations (Hilitzer 1925; Ochsner 1928; Barkman 1958; Wirth 1968). It should also be noted that, in addition to the two *Lobarion pulmonariae* associations, *Lobaria pulmonaria* is a diagnostic species for several other associations, including *Anaptychio ciliaris-Lobarietum pulmonariae* (class *Physcietea*), *Cetrario laureri-Lobarietum pulmonariae* (Zhuravleva et al. 2004), and *Parmelio tiliacei-Lobarietum pulmonariae* (newly described here, class *Hypogymnietea physodis*). Rare and unique communities of *Lobarion pulmonariae*, which can be reliably identified only by the presence of diagnostic lichen species, require further detailed study. Lichen communities that develop on bryophytes align well with the European lichen-bryophyte syntaxa scheme of the order *Antitrichietalia curtipendulae* (class *Neckeretea complanatae*). Neither *Nephrometum belli* nor *Lobarion pulmonariae* have been documented in Ukraine.

Cluster C, which includes substrate hygrophilous lichen communities on mosses, primarily includes crustose lichen species. Superficially, it resembles *Lobarion pulmonariae* communities. However, the communities of this cluster are mesothermophilic and develop in the middle

forest belt on mosses growing on tree bark, whereas the typical *Lobarion pulmonariae* community is psychrophilous (at least in Central Europe) and predominantly composed of foliose macrolichens developing on bryophyte cushions. Considering the significant differences in species composition, we propose classifying this community within a separate alliance, *Biatorion vernalis*, with *Biatora vernalis*, *Normandina acroglypta*, *Normandina pulchella* and *Strigula stigmatella* as its characteristic species. Different interpretations of the code prevent us from answering unequivocally whether epiphytic communities on mosses are syntaxa. In our opinion, bryophytes are considered substrate on the same level as bark, leaves, and wood, and are included in the broad concept of epiphytes. However, we will leave these communities as provisional syntaxonomical units (*Biatorion vernalis* and *Biatoro vernali-Striguletum stigmatellae*) until the discussion of relevant changes and clarifications in the ICPN.

Cluster E – nitrophilous communities (*Physcietea*)

The lectotype of the association *Physcietum adscendentis*, which is the nomenclature type of the alliance *Xanthorion parietinae*, originally described from the vicinity of Zurich on *Populus nigra* (Ochsner 1928), shares a similar species composition with the lectotype of the association *Parmelietum trichotero-scorteae* (Barkman 1958). However, none of our community clusters included these relevés during the analysis. It is also notable that the holotype and one relevé of the OD of the association *Lecanoretum carpinea montanum* (Barkman 1958) were included in the cluster of the class *Physcietea*. Traditionally, these communities were assigned to the class *Arthonio radiatae-Lecidelletea elaeochromae* as part of a distinct alliance *Lecanorion carpineae* (Mucina et al. 2016). However, the presence of species that can grow on eutrophicated bark, such as *Caloplaca cerina* and *Candelariella xanthostigma*, also connects these plots to the class *Physcietea*. The relevés on beeches bark that we sampled in the Ukrainian Carpathians did not correspond to this community. Additionally, the association *Anaptychio ciliaris-Lobarietum pulmonariae* (Zhuravleva et al. 2004), described from the Urals, also appears among the communities of the class *Physcietea*. The frequent presence of the large leafy lichen *Lobaria pulmonaria* in these communities often misleads researchers, leading them to mistakenly assign these communities to the *Lobarion pulmonariae*. However, the presence of a significant number of nitrophilic lichen species from the family *Physciaceae* in this association, as well as the species *Collema nigrescens* and *Leptogium saturninum*, makes it more closely related to *Physcietum adscendentis*. In our case, the ordination places the relevés closer to the Lobarion.

The presented strongly nitrophilic communities on the bark of old-growth *Fagus sylvatica* are rare and have a species composition distinct from those described in the lowland southern regions of Ukraine (Khodosovtsev et al. 2017. These communities include the widespread beech bark species *Lecanora argentata*, the endophloeic pioneer species *Arthonia punctiformis* and *Arthopyrenia punctiformis*, as well as several nitrophilic species, such as *Candelaria concolor*. In this paper, we provisionally designate this cluster as *Candelarietum concoloris* (Gallé 1933, 1976) until the results of a comprehensive revision of the *Xanthorion parietinae* in Ukraine become available.

Cluster F – acidophilous communities (*Hypogymnietea physodis*)

(Figure 4)

We compared communities from the Carpathians with the *Pseudoevernio furfuracea-Hypotrachynetum afrorevolutae* (type for *Parmelion perlatae*), but none of our relevés fall into these communities. We assign the epiphytic lichen communities on the acidic bark of *Fagus sylvatica* to the *Parmelion physodis* alliance. The communities, represented in clusters F4 and F5, develop at the upper limits of *F. sylvatica* distribution in the Carpathians. They have no known analogues among other communities of the class. Ecologically, these communities are quite similar, but they likely differ in terms of acidity and nitrophily. The *Japewio aliphatici-Parmelietum saxatilis* (Cluster F4) is acidophilous, with *Biatora efflorescens*, *Fuscidea pusilla*, *Japewia aliphatica*, *Violella fucata*, and *Scoliciosporum umbrinum* as differential species. In contrast, the *Parmelio tiliacei-Lobarietum pulmonariae* (Cluster F5) communities are more or less neutrophilic and slightly nitrophilic, with *Parmelia tiliacea*, *Lobaria pulmonaria*, *Cetrelia monachorum*, *Physconia enteroxantha*, and *Phaeophyscia endophoenicea* as differential species.

Cluster G – anitrophilous species-rich communities (*Arthonio radiatae-Lecidelletea elaeochromae*)

(Figure 3)

The lectotypes and some relevés from the OD of the associations *Pertusarietum amarae*, *Pyrenuletum nitidae*, and *Thelotremetum lepadinii* (Hilitzer 1925; Barkman 1958) are described from a beech forest with a significant proportion of conifers (e.g. *Picea abies*) near Nový Svět (Czech Republic). These were assigned to the subcluster G3 during the second stage of analysis. Almost all relevés, except for those dominated by *Phlyctis argena*, *Pyrenula nitida*, and *Graphis scripta* (the typical species of the class), also included diagnostic species of the *Hypogymnion physodis* alliance, particularly *Hypogymnia physodes*, *Parmelia saxatilis* s.l., and *Platismatia glauca*, which were recorded with high frequencies. The analysis suggests that these three associations are difficult to separate and probably synonyms. They have not yet been recorded from the Ukrainian Carpathians. The holotype of the species-poor oceanic community *Opegraphetum diaphorae* Barkman 1958 also falls within the subcluster G3, but is most likely not synonymous with the others and requires further study. All these associations differ significantly in their species composition from the neutrophilic epiphytic lichen communities *Thelotremo lepadini-Biatoretum ponticae* (subcluster G5) that develop on the bark of old beeches in primeval Carpathian forests. In contrast, *Buellio griseovirenti-Bacidinetum sulphurellae* covers the bark of young beeches (30–60 years old), particularly in areas where beech forests are being restored and stands

of uniform age are formed. In addition, the list of diagnostic species (EVC) of the *Arthonio radiatae-Lecidelletea elaeochromae* needs revision, because some of the included species are not always confirmed by phytosociological reflection in this class (Table 1), e.g. *Buellia disciformis* and *Lepra amara*.

New syntaxa and lectotypification

Note: The numbers in brackets refer to the species cover in percent.

***Biatoretum radicicolae* Khodosovtsev, Vondrák et Kuzemko ass. nov. hoc loco**

Holotypus: relevé number 10 (876 in TURBOVEG database), Suppl. material 1, cluster A [*Agonimia repleta* (10), *Biatora radicicola* (5), *B. chrysantha* (5), *B. efflorescens* (1), *Bacidia subincompta* (1), *Bryostigma muscigenum* (1), *Catinaria atropurpurea* (5), *Gyalideopsis helvetica* (1), *Lepraria finkii* (1), *L. jackii* (1), *Porpidia macrocarpa* (1), *Verrucaria hegetschweileri* (1), *V. viridigrana* (1)]: Ukraine, Zakarpattia region, Tyachiv District, Carpathian Biosphere Reserve, Shyrokiy Luh massive, 1218 m a.s.l., 48.31188°N, 23.69985°E, plot SL4, *Fagus sylvatica*, on exposed root, N exposition, field number 809X10b, 19 May 2019, O. Khodosovtsev, J. Vondrák.

Diagnostic species: *Agonimia repleta*, *Biatora chrysantha*, *B. radicicola*, *Caloplaca sorocarpa*, *Catinaria atropurpurea*, *Gyalideopsis helvetica*, *Lepraria jackii*, *P. macrocarpa* (corticolous form).

Note: Refers to the cluster A.

***Biatoro vernali-Striguletum stigmatellae* Khodosovtsev, Vondrák et Kuzemko ass. nov. prov.**

Holotypus: relevé number 64 (1006 in TURBOVEG database), Suppl. material 1, cluster C [*Anisomeridium polypori* (1), *Biatora vernalis* (5), *Cladonia coniocreae* (1), *Lepraria finkii* (40), *Normandina acroglypta* (1), *N. pulchella* (3), *Strigula stigmatella* (1), *Vezdaea aestivalis* (1)]: Zakarpattia region, Tyachiv District, Carpathians Biosphere Reserve, Shyrokyi Luh massive, 587 m a.s.l., 48.30741°N, 23.73316°E, plot SL-1, *Fagus sylvatica*, 30 cm diameter, SE exposition, on mosses at the base of the tree, field number 743X11a, 24 May 2019, O. Khodosovtsev.

Diagnostic species: *Biatora vernalis*, *Lepraria finkii*, *Strigula stigmatella*.

Note: Refers to the subcluster C.

***Buellio griseovirenti-Bacidinetum sulphurellae* Khodosovtsev, Vondrák et Kuzemko ass. nov. hoc loco**

Holotypus: relevé number 90 (796 in TURBOVEG database), Suppl. material 4: subcluster G4 [*Arthopyrenia punctiformis* (5), *Phlyctis argena* (15), *Bacidina sulphurella* (1), *Buellia griseovirens* (20), *Graphis scripta* (5), *Lecanora pulicaris* (1), *Lepraria finkii* (1)]: Zakarpattia region, Khust District, National Nature Park "Zacharovanyi Kray," Molochnyi Kamin, young beech forest, 796 m a.s.l., 48.44470°N, 23.09254°E, plot I-2, *Fagus sylvatica*, 22 cm diameter, on bark, field number I-2-3b, 8 September 2023, O. Khodosovtsev, J. Vondrák, S. Svoboda.

Diagnostic species: *Bacidina sulphurella*, *Buellia griseovirens*, *Fuscidea pusilla*, *Graphis scripta*, *Lecania croatica*, *Lepraria finkii*, *Melanelixia glabratula*, *Micarea micrococca*.

Note: Refers to the subcluster G4.

***Dictyocatenulatetum albae* Khodosovtsev, Vondrák et Kuzemko ass. nov. hoc loco**

Holotypus: relevé number 25 (1084 in TURBOVEG database), Suppl. material 1, subcluster B1 [*Arthonia helvola* (3), *Dictyocatenulata alba* (10), *Cladonia coniocrea* (1)]: Zakarpattia region, Khust District, National Nature Park "Zacharovanyi Kray," Velykyi Dil massive, 906 m a.s.l., 48.40932°N, 23.17617°E, plot VD-1, *Fagus sylvatica*, on exposed root at the base of the tree, field number VD10b, 12 August 2024, O. Khodosovtsev, E. Khymych.

Diagnostic species: *Agonimia repleta*, *Arthonia helvola*, *A. spadicea*, *Dictyocatenulata alba*.

Note: Refers to the subcluster B1.

***Japewio aliphatici-Parmelietum saxatilis* Khodosovtsev, Vondrák et Kuzemko ass. nov. hoc loco**

Holotypus: relevé number 30 (875 in TURBOVEG database), Suppl. material 3, subcluster F4 [*Arthonia mediella* (1), *Arthonia radiata* (1), *Biatora efflorescens* (1), *Biatora ocelliformis* (1), *Buellia griseovirens* (1), *Candelariella efflorescens* (3), *Japewia aliphatica* (5), *Lecanora pulicaris* (1), *Lecidella elaeochroma* (1), *Lepra amara* (1), *Lepraria finkii* (1), *Loxospora elatina* s. l. (1), *Melanohalea elegantula* (15), *Hypogymnia physodes* (10), *Parmelia saxatilis* (10), *Parmelia sulcata* (5), *Parmeliopsis ambigua* (15), *Parmeliopsis hyperopta* (2), *Parmelina pastillifera* (1), *Phlyctis argena* (3), *Platismatia glauca* (5), *Pseudoschismatomma rufescens* (1), *Ramalina fastigiata* (1), *Ramalina pollinaria* (1), *Rinodina sophodes* (2), *Rinodina subpariata* (1), *Ropalospora viridis* (1), *Scoliciosporum umbrinum* (1)]: Ukraine, Zakarpattia region, Tyachiv District, Carpathian Biosphere Reserve, Shyrokiy Luh massive, 1218 m a.s.l., 48.31188°N, 23.69985°E, plot SL4, *Fagus sylvatica*, on bark, N exposition, field number 809X10a, 19 May 2019, O. Khodosovtsev, J. Vondrák.

Diagnostic species: *Biatora efflorescens*, *Buellia disciformis*, *B. griseovirens*, *Fuscidea pusilla*, *Japewia aliphatica*, *Melanohalea elegantula*, *Parmelia saxatilis*, *Parmelina pastillifera*, *Parmeliopsis ambigua*, *Platismatia glauca*, *Pseudevernia furfuracea*, *Scoliciosporum umbrinum*.

Note: Refers to the subcluster F4.

***Parmelio tiliacei-Lobarietum pulmonariae* Khodosovtsev, Vondrák et Kuzemko ass. nov. hoc loco**

Holotypus: relevé number 47 (841 in TURBOVEG database), Suppl. material 3, subcluster F4 [*Anaptychia ciliaris* (1), *Arthonia vinosa* (1), *Bacidia circumspecta* (1),

Bacidia subincompta (1), *Buellia griseovirens* (3), *Cetrelia monachorum* (1), *Hypogymnia physodis* (1), *Lecanora carpinea* (1), *Lecidella elaeochroma* (1), *Lepra amara* (3), *L. incana* (1), *Lobaria pulmonaria* (10), *Melanelixia glabratula* (1), *Melanohalea eleganthula* (1), *Parmelia saxatilis* (40), *Parmelia submontana* (3), *P. sulcata* (15), *Parmelina tiliacea* (7), *Parmeliopsis ambigua* (3), *Pertusaria coronata* (1), *Phaeophyscia endophoenicea* (1), *Phlyctis argena* (3), *Platysmatia glauca* (3), *Ramalina europea* (1), *Ramalina farinaceae* (1), *Ramalina fraxinea* (3)]: Zakarpattia region, Irshava District, near polonyna Borzhava, beech forest near subalpine grasslands, 1221 m a.s.l., 48.61054°N, 23.21180°E, plot Borzhava-1, *Fagus sylvatica*, on bark, 90 cm diameter, 10 September 2023, O. Khodosovtsev, J. Vondrák et S. Svoboda.

Diagnostic species: *Buellia griseovirens*, *Cetrelia monachorum*, *Lecanora argentata*, *L. pulicaris*, *Lepra amara*, *Lobaria pulmonaria*, *Melanelixia glabra*, *Myriolecis sambuci*, *Parmelia saxatilis*, *P. submontana*, *P. sulcata*, *Parmelina tiliacea*, *Phaeophyscia endophoenicea*, *Phlyctis argena*, *Physconia enteroxantha*, *Platismatia glauca*, *Pseudevernia furfuracea*, *Ramalina europaea*, *Ramalina farinacea*.

Note: Refers to the subcluster F5.

***Thelotremo lepadini-Biatoretum ponticae* Khodosovtsev, Vondrák et Kuzemko ass. nov. hoc loco**

Holotypus: relevé number 97 (787 in TURBOVEG database), Suppl. material 4, subcluster G5 [*Biatora pontica* (3), *Catinaria atropurpurea* (1), *Cetrelia monachorum* (10), *Chicitaea cristinae* (3), *Cladonia coniocreae* (3), *Coenogonium luteum* (1), *Graphis scripta* (5), *Lecanora thysanophora* (5), *Lepra amara* (1), *Lepraria finkii* (3), *Lopadium disciforme* (5), *Megalaria pulverea* (1), *Melanelixia glabratula* (1), *Menegazzia terebrata* (15), *Phlyctis argena* (25), *Thelotrema lepadinum* (7)]: Zakarpattia region, Khust District, National Nature Park "Zacharovanyi Kray," Irshavka site, 746 m a.s.l., 48.45196°N, 23.08474°E, plot Irshava-1, *Fagus sylvatica*, 76 cm diameter, on bark of the living tree, field number I15b, 7 September 2023, O. Khodosovtsev, J. Vondrák, S. Svoboda.

Diagnostic species: *Anisomeridium polypori*, *Biatora pontica*, *Graphis scripta*, *Lecanora thysanophora* (character species), *Loxospora elatina* s. lat. (incl. *Chicitaea cristinae*), *Phlyctis argena*, *Pyrenula nitida*, *Thelotrema lepadinum*, *Zwackhia viridis*.

Note: Refers to the subcluster G5.

***Biatorion radicicolae* Khodosovtsev, Vondrák et Kuzemko all. nov. hoc loco**
(*Agonimietalia repletae*, *Agonimietea repletae*)

Holotypus hoc loco: Biatoretum radicicolae Khodosovtsev, Vondrák et Kuzemko hoc loco, relevés in subcluster A (Suppl. material 1).

Character species of the alliance: *Agonimia repleta*, *Biatora radicicola*, *B. chrysantha*, *Caloplaca sorocarpa*, *Porpidia macrocarpa* (corticolous form), *Verrucaria hegetschweileri*.

Synecology: Neutrophilous to moderately acidophilous, slightly nitrophilous, ombrophilous, hygrophilous, heliophilous, epiphytic lichen communities on the naked roots and the base of old deciduous trees with smooth bark (e.g. *Fagus sylvatica*) near subalpine line (1150–1340 m a.s.l.).

Synchorology: Carpathians (Central Europe).

***Biatorion vernalis* Khodosovtsev, Vondrák et Kuzemko all. nov. prov.**
(*Agonimietalia repletae*, *Agonimietea repletae*)

Holotypus hoc loco: Biatoro vernali-Striguletum stigmatellae Khodosovtsev, Vondrák et Kuzemko *prov.*, relevés in cluster C (Suppl. material 1).

Character species of the alliance: *Biatora vernalis*, *Strigula stigmatella*.

Synecology: Anitrophilous, neutrophilous to moderately acidophilous, mesotermophilous, substratohygrophilous, ombrophilous, moderately sciophilous, lichen communities with predominance of crustose lichens on bryophytes on old trees with smooth bark (*e.g. Fagus sylvatica*) in mountain belt (500–1100 m a.s.l.).

Synchorology: Carpathians (Central Europe).

***Dictyocatenulation albae* Khodosovtsev, Vondrák et Kuzemko all. nov. hoc loco**
(*Agonimietalia repletae*, *Agonimietea repletae*)

Holotypus hoc loco: Dictyocatenulatetum albae Khodosovtsev, Vondrák et Kuzemko hoc loco, relevés in subcluster B1 (Suppl. material 1).

Character species of the alliance: *Anisomeridium macrocarpum*, *Arthonia helvola*, *Dictyocatenulata alba*, *Gyalecta herculina*.

Synecology: Anitrophilous, neutrophilous, mesotermophilous, hygrophilous, ombrophilous, sciophilous, mesothermophilous, epiphytic lichen communities on exposed roots and the base of deciduous trees with smooth bark (e.g. *Fagus sylvatica*) in montane belt (700–1200 m a.s.l.).

Synchorology: Carpathians (Central Europe).

***Agonimietalia repletae* Khodosovtsev, Vondrák et Kuzemko ord. nov. hoc loco**
(*Agonimietea repletae*)

Holotypus hoc loco: Biatorion radicicolae Khodosovtsev, Vondrák et Kuzemko hoc loco, relevés in cluster A, B and C (Suppl. material 1).

Diagnostic species of the order: *Anisomeridium macrocarpum* (character species), *Arthonia helvola*, *A. spadicea*, *Agonimia repleta*, *Aspicilia laevata* (corticolous form, character species), *Bacidia subincompta*, *Biatora radicicola*, *B. chrysantha*, *B. vernalis*, *Brianaria tuberculata* (corticolous form, character species), *Caloplaca sorocarpa*, *Catinaria atropurpurea*, *Dictyocatenulata alba*, *Gyalecta herculina*, *Gyalideopsis helvetica*, *Lepraria jackii*, *Porpidia macrocarpa* (corticolous form), *Strigula stigmatella*, *Tetramelas chloroleucus* (character species), *Verrucaria hegetschweileri* (character species), *V. viridigrana* (character species).

Synecology: Epiphytic lichen communities on exposed roots and the bases of deciduous trees with smooth bark (e.g. *Carpinus betulus*, *Fagus sylvatica*).

Synchorology: Carpathians (Central Europe).

***Agonimietea repletae* Khodosovtsev, Vondrák et Kuzemko cl. nov. hoc loco**

Holotypus hoc loco: *Agonimietalia repletae* Khodosovtsev, Vondrák et Kuzemko hoc loco, relevés in clusters A and B (Suppl. material 1).

Diagnostic species of the class: *Anisomeridium macrocarpum* (character species), *Arthonia helvola*, *A. spadicea*, *Agonimia repleta*, *Aspicilia laevata* (corticolous form, character species), *Bacidia subincompta*, *Biatora radicicola*, *B. chrysantha*, *B. vernalis*, *Brianaria tuberculata* (corticolous form, character species), *Caloplaca sorocarpa*, *Catinaria atropurpurea*, *Dictyocatenulata alba*, *Gyalecta herculina*, *Gyalideopsis helvetica*, *Lepraria jackii*, *Porpidia macrocarpa* (corticolous form), *Strigula stigmatella*, *Tetramelas chloroleucus* (character species), *Verrucaria hegetschweileri* (character species), *V. viridigrana* (character species).

Synecology: Epiphytic lichen communities on exposed roots and the base of deciduous trees with smooth bark (e.g. *Carpinus betulus*, *Fagus sylvatica*).

Synchorology: Carpathians (Central Europe).

***Candelarietum concoloris* Gallé 1933**

Lectotypus hoc loco: Gallé, 1976, A Móra Ferenc Múzeum Évkönyvei, 77: page 472, table 4, relevé 10 [*Candelaria concolor* (37), *Physcia adscendens* (3), *Physcia aipolia* (3), *Physcia stellaris* (3), *Physcia tenella* (3), *Lecanora argentata* (= *Lecanora subfusca*) (3), *Lecidella elaeochroma* (3), *Lecanora chlarotera* (3)]: Hungary, Csongrád megye, Deszk, arboretum, 83 m. s. m., 46.216250°N, 20.237139°E, on *Aesculus hippocastanum*, 10 September 1930, L. Gallé.

Diagnostic species: *Candelaria concolor*, *Lecanora argentata*, *Lecidella elaeochroma*, *Lecanora chlarotera*.

Syntaxonomic scheme of epiphytic lichen communities in the old-growth beech forests of western Ukraine

Class *Agonimietea repletae* Khodosovtsev, Vondrák et Kuzemko (this paper)
- Order *Agonimietalia repletae* Khodosovtsev, Vondrák et Kuzemko (this paper)
  - Alliance *Biatorion radicicolae* Khodosovtsev, Vondrák et Kuzemko (this paper)
    - Ass. *Biatoretum radicicolae* Khodosovtsev, Vondrák et Kuzemko (this paper)
  - Alliance *Dictyocatenulation albae* Khodosovtsev, Vondrák et Kuzemko (this paper)
    - Ass. *Dictyocatenulatetum albae* Khodosovtsev, Vondrák et Kuzemko (this paper)
    - Comm. *Gyalecta herculina*

Class *Arthonio radiatae-Lecidelletea elaeochromae* Drehwald 1993
- Order *Graphidetalia scriptae* Hadač in Klika et Hadač 1944
  - Alliance *Graphidion scriptae* Ochsner ex Felfoldy 1941
    - Ass. *Porinetum carpineae* Barkman 1958
    - Ass. *Buellio griseovirenti-Bacidinetum sulphurellae* Khodosovtsev, Vondrák et Kuzemko (this paper)
    - Ass. *Thelotremo lepadini-Biatoretum ponticae* Khodosovtsev, Vondrák et Kuzemko (this paper)

Class *Physcietea* Tomaselli et DeMicheli 1952
- Order *Physcietalia* Hadač in Klika et Hadač 1944
  - Alliance *Xanthorion parietinae* Ochsner 1928
    - Ass. *Candelarietum concoloris* Gallé 1933
    - Derivative comm. *Physcia tenella* + *Parmelium saxatilis* + *Caloplaca sorocarpa*

Class *Hypogymnietea physodis* Follmann 1974
- Order *Alectorietalia* Dahl et Hadač in Klika et Hadač 1944
  - Alliance *Parmelion physodis* von Krusenstjerna 1945
    - Ass. *Japewio aliphatici-Parmelietum saxatilis* Khodosovtsev, Vondrák et Kuzemko (this paper)
    - Ass. *Parmelio tiliacei-Lobarietum pulmonariae* Khodosovtsev, Vondrák et Kuzemko (this paper)
    - Derivative comm. *Platismatia glauca* + *Loxospora elatina*.
    - Incertae sedis communities on bryophytes (probable, refer to *Agonimietea repletae*)
  - Alliance *Biatorion vernalis* Khodosovtsev, Vondrák et Kuzemko all. prov. (this paper)
    - Ass. *Biatoro vernali-Striguletum stigmatellae* Khodosovtsev, Vondrák et Kuzemko ass. prov. (this paper)

Conclusions

Based on syntaxonomical analysis, epiphytic lichen communities on *Fagus sylvatica* in the old-growth beech forests of the Ukrainian Carpathians are classified into four classes: *Agonimietea repletae*, *Arthonio radiatae-Lecidelletea elaeochromae*, *Physcietea*, and *Hypogymnietea physodis*. *Agonimietea repletae* and *Agonimietalia repletae* represent a newly proposed class and order, respectively, encompassing lichen communities developing on the exposed root systems and bases of old beeches. Two newly described alliances are: 1) *Biatorion radicicolae* encompassing hygrophilous, slightly nitrophilous, heliophilous, and psychrophilous lichen communities that develop on the exposed roots of old trees with smooth bark near the tree line; and

2) *Dictyocatenulation albae* including hygrophilous, anitrophilous, sciophilous, and mesothermophilous lichen communities that occur on the exposed roots and bases of old trees with smooth bark in the montane belt. The alliance *Biatorion vernalis*, grouping substrate hygrophilous, mesothermophilous, moderately sciophilous, and anitrophilous lichen communities growing on mosses in the montane belt, was proposed as provisional. Five new associations were described, and one was proposed as provisional.

The associations *Japewio aliphatici-Parmelietum saxatilis*, *Parmelio tiliacei-Lobarietum pulmonariae*, *Thelotremo lepadini-Biatoretum ponticae*, and transitional communities between classes (derivative communities) represent lichen hotspots. The communities *Thelotremo lepadini-Biatoretum ponticae* (*Graphidion scriptae*), *Dyctiocatenulatetum albae* (*Dyctiocatenulation albae*), and *Biatoretum vernalis* (*Biatorion vernalis*) occur predominantly in primeval beech forests, apparently preferring the absence of any forest management, and can be used as indicators of the ecological integrity of beech forest habitats.

Data availability

All data are available in this paper.

Author contributions

OKh conceived of the scientific idea and designed the study. OKh, JV and AK collected data. OKh and AK performed the statistical analyses. OKh drafted the initial manuscript. All authors discussed the methodology and results and contributed to writing the final manuscript.

Acknowledgements

The authors are grateful to anonymous reviewers for their critical notes on the manuscript; Evelina Khymych, Valerii Darmostuk, Stanislav Svoboda, Zdeněk Palice, Jiří Malíček, Ondřej Peksa, and František Bouda for their help with lichens in the field; Alla Zitenyuk for her help with the map; Vasyl Mochan, Yaroslav Petrashuk, Illia Chorney, Mykhailo Drebet, Vitaliy Stratiy, and Vasyl Pokynchereda for their help organizing the expeditions to the Gorgany Nature Reserve, Carpathian Biosphere Reserve, Zacharovanyi Krai, Vyzhnytskiy, and Podilski Tovtry National Nature Parks. Oleksandr Khodosovtsev's work on the publication was supported by the National Research Foundation of Ukraine (Project 2022.02/0007 Resistance of Epiphytic Lichen Communities in Old-growth and Primeval Forests of the Ukrainian Carpathians to Global Climate Change and Regional Management). Jan Vondrák received support by long-term research development grant RVO 67985939.

References

Abbassi Maaf L, Roux C (1987) Les peuplements lichéniques corticoles de la chênaie verte: étude comparée de la gardiole de Rians et de l'île de Port-Cros (Var). Bulletin de la Société linnéenne de Provence 38: 189–245.

Almborn O (1948) Distribution and ecology of some South Scandinavian lichens. Botaniska Notiser 1(2): 1–254.

Barkman JJ (1958) Phytosociology and ecology of cryptogamic epiphytes. Van Gorcum, Assen, NL.

Breuss O (1998) Eine neue *Verrucaria*-Art mit Goniocystenthallus. Linzer Biologische Beitraege 30: 277–279.

Bültmann H, Roux C, Egea J, Julve P, Bricaud O, Giaccone G, Täuscher L, Creveld M, Di Martino V, … Takeuchi N (2015) Validations and descriptions of European syntaxa of vegetation dominated by lichens, bryophytes and algae. Lazaroa 36: 107–129. https://doi.org/10.5209/rev_LAZA.2015.v36.51255

Chytrý M, Tichý L (2003) Diagnostic, constant and dominant species of vegetation classes and alliances of the Czech Republic: a statistical revision. Folia Facultatis Scientiarum Naturalium Universitatis Masarykianae Brunensis, Biologia 108: 1–231.

Chytrý M, Tichý L, Holt J, Botta-Dukát Z (2002) Determination of diagnostic species with statistical fidelity measures. Journal of Vegetation Science 13: 79–90. https://doi.org/10.1111/j.1654-1103.2002.tb02025.x

Chytrý M, Tichý L, Hennekens SM, Knollová I, Janssen JAM, Rodwell JS, Peterka T, Marcenò C, Landucci F, … Schaminée JHJ (2020) EUNIS habitat classification: expert system, characteristic species combinations and distribution maps of European habitats. Applied Vegetation Science 23: 648–675. https://doi.org/10.1111/avsc.12519

Commarmot B, Brändli U-B, Hamor F, Lavnyy V (2013) Inventory of the largest primeval beech forest in Europe: a Swiss-Ukrainian scientific adventure. WSL Swiss Federal Research Institute, Birmensdorf, CH.

Czarnota P, Coppins BJ (2000) A new species of *Agonimia* and some interesting lichens from Gorce Mts (Western Beskidy Mts) new to Poland. Graphis Scripta 11: 56–60.

Delzenne C, Gehu JM (1978) Sur deux associations épiphytes du *Parmelion caperatae* des plaines et collines françaises. Documents Phytosociologiques 2: 117–126.

Drehwald U (1993) Die Pflanzengesellschaften Niedersachsens: Bestandsentwicklung, Gefährdung und Schutzprobleme. Naturschutz und Landschaftspflege in Niedersachsen 20(10): 1–124.

Dymytrova L, Nadyeina O, Naumovych A, Keller C, Scheidegger C (2013) Primeval beech forests of Ukrainian Carpathians are sanctuaries for rare and endangered epiphytic lichens. Herzogia 26: 73–89. https://doi.org/10.13158/heia.26.1.2013.73

Gallé L (1933) Lichenassoziationen aus Szeged. Flechtenassoziationen aus dem Baron Gerliczyschen Park zu Deszk. Acta Biolica Szegedienis 2: 195–211.

Gallé L (1976) Magyarország zuzmócönózisai [Flechtenassoziationen in Ungarn]. A Móra Ferenc Múzeum Évkönyvei 77: 429–493. [in Hungarian]

Gauslaa Y (1995) The *Lobarion*, an epiphytic community of ancient forests threatened by acid rain. Lichenologist 27: 59–76. https://doi.org/10.1006/lich.1995.0005

Hennekens SM, Schaminée JHJ (2001) TURBOVEG, a comprehensive database management system for vegetation data. Journal of Vegetation Science 12: 589–591. https://doi.org/10.2307/3237010

Hilitzer A (1925) La végétation épiphyte de la Bohème. Publications de la Faculté des sciences de L'université Charles, Prague 41: 1–200.

Hurtado P, Aragón RG, Martínez I, Mayrhofer H, Prieto M (2023) The epiphytic lichens on *Fagus sylvatica* in beech forests of Europe: towards an open and dynamic checklist. Mediterranean Botany 44: e84299. https://doi.org/10.5209/mbot.84299

James PW, Hawksworth DL, Rose F (1977) Lichen communities in the British Isles: a preliminary conspectus. In: Seaward MRD (Ed.) Lichen Ecology. Academic Press, London, UK, 295–413.

Khodosovtsev AY, Maliuga NG, Darmostuk VV, Khodosovtseva AY, Klymenko VM (2017) The corticolous *Physcietea* lichen communities in the old parks of Kherson region (Ukraine). Chornomorski Botanical Journal 13: 481–515. https://doi.org/10.14255/2308-9628/17.134/6

Khodosovtsev A, Darmostuk V, Prylutskyi O, Kuzemko A (2022) Silicicolous lichen communities of the Ukrainian Crystalline Shield. Applied Vegetation Science 25: e12699. https://doi.org/10.1111/avsc.12699

Khodosovtsev A, Darmostuk V, Kondratyuk S (2023) *Xanthoria tendraensis* sp. nov. and *Xanthorietum tendraensis* ass. nova from the northern Black Sea coast (Ukraine). Folia Geobotanica 58: 109–126. https://doi.org/10.1007/s12224-023-09430-9

Khodosovtsev OYe, Palice Z, Maliček J, Svoboda S, Darmostuk VV, Peksa O, Bouda F, Vondrák J (2024) First Ukrainian records of lichens and lichenicolous fungi from Carpathian primeval forests. Czech Mycology 76: 191–213. https://doi.org/10.33585/cmy.76206

Klement O (1955) Prodromus der mitteleuropäischen Flechtengesellschaften. Feddes Repertorium 135: 5–194.

Kondratyuk SY, Coppins BJ (1999) Basement for the lichen monitoring in Uzhansky National Nature Park, Ukrainian Part of the Biosphere Reserve «Eastern Carpathians». Roczniki Bieszczadzkie 8: 149–192.

Kondratyuk SY, Coppins BJ, Zelenko SD, Khodosovtsev AY, Coppins B, Wolseley PA (1997) Lobarion lichens as indicators of primeval forests in the Ukrainian part of the International Biosphere Reserve «Eastern Carpathians»: distribution, ecology, long-term monitoring and recommendations for conservation. Roczniki Bieszczadzkie 6: 65–87.

Kuzemko A (2016) Classification of the class *Molinio-Arrhenatheretea* in the forest and forest-steppe zones of Ukraine. Phytocoenologia 46: 241–256. https://doi.org/10.1127/phyto/2016/0083

Malíček J, Palice Z, Acton A, Berger F, Bouda F, Sanderson N, Vondrák J (2018) Uholka primeval forest in the Ukrainian Carpathians – a keynote area for diversity of forest lichens in Europe. Herzogia 31: 140–171. https://doi.org/10.13158/099.031.0110

Mucina L, Bültmann H, Dierßen K, Theurillat JP, Raus T, Čarni A, Šumberová K, Willner W, Dengler J, … Tichý L (2016) Vegetation of Europe: hierarchical floristic classification system of vascular plant, bryophyte, lichen, and algal communities. Applied Vegetation Science 19(suppl. 1): 3–264. https://doi.org/10.1111/avsc.12257

Nimis PL (2025) ITALIC – The Information System on Italian Lichens. Version 8.0. University of Trieste, Department of Biology. https://dryades.units.it/italic [accessed 21 Jan 2025]

Nimis PL, Hafellner J, Roux C, Clerc P, Mayrhofer H, Martellos S, Bilovitz PO (2018) The lichens of the Alps – an annotated checklist. MycoKeys 31: 1–634. https://doi.org/10.3897/mycokeys.31.23568

Ochsner F (1928) Studien über die Epiphyten-Vegetation der Schweiz. Jahrbuch der St. Gallischen Naturwissenschaftlichen Gesellschaft für das Vereinsjahr 63: 1–106.

Oksanen AJ, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, … Wagner H (2018) Vegan: community ecology package. https://doi.org/10.4135/9781412971874.n145 [accessed 21 Jan 2025]

Printzen C, Halda JP, McCarthy JW, Palice Z, Rodriguez-Flakus P, Thor G, Tønsberg T, Vondrák J (2016) Five new species of *Biatora* from four continents. Herzogia 29: 566–585. https://doi.org/10.13158/heia.29.2.2016.566

R Core Team (2025) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/

Roleček J, Tichý L, Zelený D, Chytrý M (2009) Modified TWINSPAN classification in which the hierarchy respects cluster heterogeneity. Journal of Vegetation Science 20: 596–602. https://doi.org/10.1111/j.1654-1103.2009.01062.x

Schubert R, Stordeur R (2011) Synopsis der Flechtengesellschaften Sachsen-Anhalts. Schlechtendalia 22: 1–88.

Smith CW, Aptroot A, Coppins BJ, Fletcher A, Gilbert OL, James PW, Wolseley PA (2009) The lichens of Great Britain and Ireland. British Lichen Society, London, UK.

Stoyko S (2002) The virgin ecosystems of Ukraine, their polyfunctional significance for nature protection. Naukovi Praci Lisivničoji Akademii Nauk Ukrajiny, Lviv, Ukraine, 27–31. [in Ukrainian]

Theurillat J-P, Willner W, Fernández-González F, Bültmann H, Čarni A, Gigante D, Mucina L, Weber H (2021) International Code of Phytosociological Nomenclature. 4th edition. Applied Vegetation Science 24: e12491. https://doi.org/10.1111/avsc.12491

Tichý L (2002) JUICE, software for vegetation classification. Journal of Vegetation Science 13: 451–453. https://doi.org/10.1111/j.1654-1103.2002.tb02069.x

Van Haluwyn C (2010) La sociologie des lichens corticoles en Europe depuis Klement (1955) et Barkman (1958). Essai de synthèse. Bull. Ass. Fr. Lichénologie 35 (2): 1–128.

von Krusenstjerna E (1945) Bladmossvegetation och Bladmossflora I Uppsala-Trakten. Acta Phytogeographica Suecica, Uppsala, SE, 1–256.

Vondrák J, Malíček J, Palice Z, Bouda F, Berger F, Sanderson N, Acton A, Pouska V, Kish R (2018) Exploiting hot-spots: effective determination of lichen diversity in a Carpathian virgin forest. PLoS ONE 13: e0203540. https://doi.org/10.1371/journal.pone.0203540

Wirth V (1968) Soziologie, Standortsökologie und Areal des *Lobarion pulmonariae* im Südschwarzwald. Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie 88: 317–365.

Wirth V (1972) Die Silikatflechten – Gemeinschaften im außeralpinen Zentraleuropa. Dissertationes Botanicae 17: 1–306.

Wirth V (1980) Flechtenflora. Ulmer, Stuttgart, DE.

Wirth V (1995) Die Flechten Baden-Württembergs. Vol. 2. Ulmer, Stuttgart, DE.

Zhuravleva SE, Solomeshch AI, Baisheva EZ (2004) Epiphytic lichen communities with *Lobaria pulmonaria* (L.) Hoffm. in the old-growth forest of the South Urals. Vegetation of Russia 6: 15–22. https://doi.org/10.31111/vegrus/2004.06.15 [in Russian]

E-mail and ORCID

Oleksandr Y. Khodosovtsev (Corresponding author, khodosovtsev@gmail.com), ORCID: https://orcid.org/0000-0002-5906-9876
Jan Vondrák (j.vondrak@seznam.cz), ORCID: https://orcid.org/0000-0001-7568-6711
Anna A. Kuzemko (anyameadow.ak@gmail.com), ORCID: https://orcid.org/0000-0002-9425-2756

Supplementary material

Supplementary material 1
Relevés of *Agonimietea repletae* and *Biatorion vernalis* (*.xlsx)
Link: https://doi.org/10.3897/VCS.149158.suppl1

Supplementary material 2
Relevés of *Physcietea* (*.xlsx)
Link: https://doi.org/10.3897/VCS.149158.suppl2

Supplementary material 3
Relevés of *Hypogymnitea physodis* (*.xlsx)
Link: https://doi.org/10.3897/VCS.149158.suppl3

Supplementary material 4
Relevés of *Arthonio radiatae-Lecidelletea elaeochromae* (*.xlsx)
Link: https://doi.org/10.3897/VCS.149158.suppl4

Supplementary material 5
Synoptic table of lichen communities (full version) (*.xlsx)
Link: https://doi.org/10.3897/VCS.149158.suppl5